ESTIMATION OF GENETIC PARAMETERS FOR BEEF CATTLE IN UK HERDS

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CONTENTS

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ABSTRACT

Data from British Simmental cattle collected by the Meat and Livestock Commission (1969-91) from 1142 herds were utilised to estimate phenotypic, genetic and environmental parameters for various performance traits. The importance of maternal effects on the performance of these animals was also evaluated. The performance traits considered in the study were birth weight, 200-day weight, 400-day weight, ultrasonic backfat depth (backfat depth) and muscling score.

Restricted Maximum Likelihood individual animal model procedure was followed throughout, accounting for all known genetic relationships, between animals, selection decisions and non random matings. Average birth weight obtained from the analysis of 31213 records was 40 kg, whilst 200-day weight and 400-day weight averaged 285 kg and 517 kg, respectively. The corresponding values for backfat depth and muscling score were 3.12 mm and 10 points, respectively.

For univariate analyses, 6 different animal models (i.e. including or excluding maternal additive genetic effects or maternal permanent environmental effects or direct-maternal genetic covariance) were fitted to determine the relative significance of these different random effects.

The average estimates (± s.e) of the direct heritability (h^2_A), the maternal heritability (h^2_M), the covariance between direct additive genetic and maternal additive genetic effects as a proportion of the phenotypic variance (c_{AM}) and the proportion of phenotypic variance ascribable to maternal permanent environmental effects (c^2) for birth weight were 0.25±0.02, 0.06±0.01, −0.05±0.01 and 0.07±0.01, respectively. The correlation between direct additive genetic and maternal additive genetic effects (r_{AM}) was −0.45.

For 200-day weight and 400-day weight, the inclusion of a direct-maternal genetic covariance did not give a significant improvement in the log likelihood. The estimates of h^2_A, h^2_M, c_{AM}, c^2 were 0.26±0.02 , 0.05±0.01, –0.02±0.01 and 0.05±0.01 for 200-day weight and 0.35±0.03, 0.04±0.01, –0.03±0.01 and 0.03±0.01 for 400-day weight as obtained from the most comprehensive model (model 6). The estimates of r_{AM} for the two traits were –0.14 and –0.27, respectively.

The estimates of genetic parameters for weight traits from univariate analyses suggested that genotype of the calf is more important in influencing weight traits than maternal effects ($h^2_A > (h^2_M+c^2)$). Maternal genetic and maternal permanent environmental effects were of equal magnitude for the three weight traits. On the whole, maternal effects ($h^2_M+c^2$) appeared to be more important for birth weight (0.13) followed by 200-day weight (0.10) and 400-day weight (0.07).

Inclusion of maternal effects into the models of analysis for backfat depth and muscling score did not improve the log likelihood significantly over a simple animal model. Backfat depth and muscling score appeared to be moderately heritable, with direct heritability estimates of 0.32±0.06 and 0.26±0.09, respectively.

Multivariate estimation of the phenotypic, genetic and environmental parameters was carried out considering two traits at a time with only a simple animal model because of the large size of the datasets involved and computationally demanding nature of the analyses. The heritability estimates for weight gains (gain from birth to 200 days, i.e. preweaning gain, gain from birth to 400 days, i.e. postnatal gain and gain from 200 to 400 days, i.e. postweaning gain) and the correlations among them and between weight gains and other performance traits were calculated from the estimates of (co)variances from the bivariate analyses. The bivariate

REML estimates of heritability for various performance traits were generally consistent with the comparable estimates from the univariate analyses. The weight gains appeared to be moderately heritable except the postweaning gain for which a low heritability was observed. The estimates of genetic correlations (r_A) of birth weight with 200-day weight and 400-day weight were 0.60 and 0.41, respectively, while the value of r_A between 200-day weight and 400-day weight was 0.96. The genetic correlations among weight gains ranged between 0.73 and 1.00. The genetic correlations between birth weight and preweaning gain, postnatal gain and postweaning gain were 0.52, 0.35 and −0.25, respectively, whilst body weights at 200 and 400 days of age were very highly genetically correlated with weight gains.

There was a weak genetic relationship between backfat depth and weight traits (r_A ranged between 0.09 and 0.22) and weight gains (r_A ranged between −0.04 and 0.23). Muscling score had moderately high estimates of the genetic correlations with weight traits (values of r_A clustered around 0.40). The relationship between muscling score and preweaning gain and postnatal gain followed the same trend as was observed between muscling score and weight traits, but an unexpected genetic correlation (0.17) was observed between muscling score and postweaning gain.

The genetic correlation between backfat depth and muscling score was 0.10.

It is concluded that there is a reasonable genetic variation for most of the performance traits included in this study for British Simmental cattle. Hence genetic improvement can be anticipated from selection for these traits. The moderate to high estimates of genetic correlation among weights at various ages suggest that selection for any one weight would result in

considerable positive change in all weights. The growth traits did not have a strong genetic relationship with backfat depth, so improvement in growth traits may not necessarily have a deleterious effect on the leanness of the carcasses. The implications of these parameter estimates for beef cattle genetic selection schemes are discussed.

CHAPTER 1

INTRODUCTION

In the UK about 60 percent of beef produced is obtained as a by-product of the dairy herd, the remainder 38 percent comes from the national suckler herd and a small proportion (2 percent) is from animals imported from Ireland (Anonymous,1993). Breeding for increased milk yield in the dairy industry has resulted in an increase in the proportion of Holstein genes, with a consequent deterioration in beef conformation of the dairy herds and of cross-bred calves. This has also adversely affected the national suckler herd which often depends on crossbred dairy heifers as replacement stock (Bryan et al., 1991).

This situation indicates a clear need for the improvement of genetic merit of crossbred calves produced by mating of beef sires to dairy cows. It also emphasises the need to maintain good standards of beef conformation in the suckler herds. Thus the selection of high quality genetically superior animals is of importance to achieve success in commercial beef production.

The potential for genetic improvement in economic traits of farm animals depends to a large extent on the magnitude of genetic variation. The knowledge of the heritabilities of and genetic correlations among performance traits is needed for formulation of effective breeding plans.

Thompson (1989) pointed out the following five important reasons for interest in heritabilities, additive genetic (co) variances and correlations: i) they provide a quantitative summary of the inheritance of traits, ii) they measure if there is enough genetic variation in a trait to make selection effective, iii) they allow consideration of alternative selection schemes such

as individual or progeny testing, iv) they enable optimisation of selection schemes by choice of population structure, v) they are needed for the incorporation of information from relatives and other traits in to breeding values estimates.

To achieve desirable results from selective breeding, the knowledge and correct understanding of the underlying biological model is a matter of vital importance. Some performance traits of beef cattle, such as birth weight or weaning weight are influenced not only by the calf 's own genetic make up and the environmental conditions experienced by the calf but also by the pre-natal and post-natal environments provided by the dam through her uterine environment, milking and mothering ability (Koch and Clark, 1956; Willham, 1963; Falconer, 1965; Koch, 1972; Baker, 1980; Willham, 1980; Wray et al., 1991; Meyer, 1992). The dam's milking and mothering ability is an environmental effect for the calf but it is influenced by the dam's genotype and the environmental conditions experienced by her both in her current gestation and calf rearing as well as throughout her lifetime. These influences on the calf's performance through dam's milking and mothering ability have genetic and environmental contributions. Therefore, the phenotypic record of a calf consists of a direct genetic component (genes received by the calf at the time of zygote formation) and a maternal effect (both genetic, and environmental) of the dam. The maternal environmental effect can, in theory be partitioned into a permanent environmental effect influencing all calves of a cow and temporary environmental effects of a particular pregnancy and calf rearing. Thus the maternal effect may contribute to the covariance of offspring with dam, covariance of full sibs, or the covariance of maternal half sibs (Falconer, 1989). The genetic basis of maternal effects has been dealt with in detail by Willham (1963) and Thompson (1976).

So the genetic variability for performance traits in mammals contains this additional complexity of maternal effects. This justifies the inclusion of maternal effects (both genetic and environmental) along with the direct effects into the selection objectives for beef cattle to obtain maximum genetic progress.

Willham (1980) and Garrick (1990) have highlighted several problems which complicate the genetic improvement programmes for various economic traits with maternal influence. They are: i) The dam contributes both the maternal effect and half of her direct genes. This leads to problems in accurately disentangling the two types of maternal contributions (embryo-transfer and cross-fostering experiments may be used to facilitate the separation of direct and maternal effects). ii) There may be a negative genetic correlation between direct and maternal effects. If a real antagonistic relationship exists between the direct and maternal effects, concurrent genetic improvement for the two effects may be sought by having two separate lines, a sire line and a dam line, with the sire line being selected for its excellent growth characteristics and the dam line for its milking and mothering ability. iii) The expression of maternal effects is sex limited and occurs late in life, a generation behind the direct effects. iv) There may be a negative environmental covariance between generations, such that a heifer calf whose dam had a good maternal ability may carry genes for good maternal ability but have inferior performance.

Mixed model methodology (best linear unbiased prediction, BLUP) is now considered the most appropriate procedure to achieve accurate estimates of breeding values for the following reasons: it provides minimum variance unbiased predictors of genetic merit; it estimates genetic and environmental effects simultaneously; it takes into account the relationship between all animals, thus accounting for the effects of selection and non-

random matings and uses all information effectively; animals can be compared across herds and years and evaluations across years facilitate monitoring of the rates of genetic progress; it provides unbiased estimates of breeding values even for those animals whose performance records are not available through the use of the additive genetic relationship information from relatives (Hill and Meyer, 1988; Kennedy et al.,1988; Wray et al.,1991). This technique has been widely used for the genetic evaluations for growth in many countries. National genetic improvement programmes based on best linear unbiased predictor procedures have been developed for at least 15 beef breeds in the United States (Benyshek et al.,1988). These mixed model procedures require unbiased and reliable estimates of genetic and environmental (co) variances. In the UK, national beef sire evaluations for various performance traits have in the past used genetic parameters pooled from the literature as reliable estimates from a comprehensive genetic model and larger datasets are not available.

The objective of the present study was to estimate precisely the phenotypic, genetic, and environmental parameters for various performance traits of British Simmental cattle using the national data. This included a) estimation of direct genetic parameters, i.e. heritabilities of and phenotypic, genetic and environmental correlations among various performance traits, b) estimation of genetic parameters due to maternal effects, i.e. maternal heritability, direct maternal genetic correlations and the estimation of maternal permanent environmental effects on these traits . A review of the literature suggested that there was not great variation in genetic parameters among breeds and so analyses were concentrated on the Simmental breed, which has one of the largest recorded beef cattle populations in Britain.

Estimates of phenotypic, genetic, and environmental parameters for various performance traits published world wide are reviewed in chapter 2. The detailed materials and methods used in the present study are presented in chapter 3, while chapter 4 contains the univariate estimates of the genetic, phenotypic and environmental parameters for different performance traits. The multivariate parameter estimates are summarised and discussed in chapter 5. The general discussion and implications from the present study are described in chapter 6.

CHAPTER 2

REVIEW OF LITERATURE

2.1 Introduction

Estimates of direct genetic parameters and those due to maternal influences on various performance traits are required in animal breeding research for the design and application of effective breeding programmes. They are also needed for the prediction of breeding values. The objectives of this study were: (i) to present a comprehensive review of the published estimates of phenotypic, genetic and environmental parameters for various beef cattle performance traits; and (ii) to highlight and emphasise the areas of beef cattle performance where further estimates of genetic parameters are needed. This review comprises the following: (a) heritability estimates (b) genetic parameter estimates due to maternal effects (c) repeatability estimates (d) phenotypic, genetic and environmental correlations among weight traits and between weight traits and backfat depth and muscling score

2.2 Heritability Estimates

Estimates of heritability (h^2) for various performance traits obtained by different procedures are not expected to be the same. This is due to the fact that different methods of estimation give values that contain different proportions of the non-additive genetic and environmental sources of variation. Most of the estimates of heritability for various performance traits (TABLES 2.1, 2.2, 2.3, 2.4) were computed using the correlation between paternal half-sibs. Carter and Kincaid (1959) pointed out that data must meet the following requirements in order for paternal half-sib correlation estimates to be accurate: (i) a large number of degrees of freedom for sires,

TABLE 2.1 Heritability estimates for birth weight

Breed	Country	Method	Estimate			Reference
			Male	Female	Combined	
HEF	USA	rPHS	0.53 (880)	-	-	1
HEF	USA	rPHS	-	-	0.45 (281)	2
HEF	USA	rPHS	-	-	1.00 (74)	2
HEF	USA	rPHS	0.72 (635)	-	-	3
HEF	USA	rPHS	0.67 (414)	-	-	4
HEF	USA	rPHS	-	0.22±0.10 (793)	-	5
HEF	USA	rPHS	0.54 (616)	-	-	6
HEF	USA	rPHS	-	-	0.57±0.19 (789)	7
HEF	USA	bOD	-	-	0.32±0.10	7
HEF	USA	rPHS	0.49±0.09 (1769)	0.57±0.12 (1693)	-	8
HEF	UK	rPHS	-	-	0.23±0.05 (2650)	9
HEF	USA	rPHS	-	0.55 (377)	-	10
HEF	USA	bOM	-	0.46 (377)	-	10
HEF	USA	rPHS	0.54±0.10 (1379)	-	-	11
HEF	USA	rPHS	0.34±0.03	0.36±0.03	-	12
HEF	Canada	rPHS	0.35 (764)	-	-	13
HEF	USA	rPHS	-	-	0.41 (14436)	14
HEF	USA	rPHS	-	-	0.28 (4423)	15
HEF	USA	rFS	-	-	0.45 (976)	15

HEF	USA	bOD	-	-	0.45	15
HEF	USA	bOS	-	-	0.21	15
ANG	USA	rPHS	-	-	0.31±0.27 (932)	7
ANG	USA	bOD	-	-	0.22±0.08	7
ANG	USA	rPHS	0.49±0.10 (1101)	0.36±0.10 (1012)	0.40±0.07 (2113)	11
ANG	USA	REMLS	0.70 (717)	-	-	16
ANG	USA	rPHS	-	-	0.19 (26426)	14
ANG	USA	rPHS	0.51±0.09	0.41±0.09	-	17
RANG	USA	rPHS	-	-	0.46±0.02 (41184)	18
SIM	USA	rPHS	-	-	0.32±0.04 (5578)	19
SIM	USA	rPHS	0.42±0.05	0.30±0.03	0.31±0.02 (17297)	20
SIM	Canada	rPHS	-	-	0.19 (4345)	21
CHA	Cuba	rPHS	-	-	0.25±0.6(212)	22
CHA	France	rPHS	0.32±0.12 (647)	-	-	23
CHA	Canada	REMLS	-	-	0.25 (1419)	24
SGT	Cuba	rPHS	-	-	0.39±0.3 (435)	22
SGT	USA	rPHS	0.38±0.12 (939)	0.24±0.10 (955)	0.32±0.07 (1894)	25
LIM	USA	rPHS	0.19±0.04	0.17±0.02	0.16±0.02 (19700)	26
BSHH	Canada	bOD/S	-	-	0.21±0.10 (892)	27
BSHH	Canada	rPHS	0.17±0.18 (327)	-	-	28
BSHH	Canada	bSS	0.30±0.13	-	-	28
SDV	Nigeria	rPHS	-	-	0.26+0.01 (23708)	29
Zebu	Nigeria	rPHS	-	-	0.28+0.01 (31488)	29

HEF, ANG and RANG	USA	rPHS	0.43±0.07	0.35±0.06	-	30
HEF, ANG and RANG	USA	rPHS	-	0.27±0.07 (779)	-	31
BS x Z	Cuba	rPHS	-	-	0.62±0.40 (1160)	22
H x Z	Cuba	rPHS	-	-	0.09±0.10 (4955)	22
CHA, BA and LIM	France	rPHS	0.31±0.06 (2673)	-	-	23
ANG and SHH	USA	rPHS	-	0.30±0.12 (647)	-	32
HEF and GHEF	USA	rPHS	-	0.37±0.07 (2092)	-	32
SBP	Canada	rPHS	0.47 (1313)	-	-	13
SBP1	Canada	rPHS	-	0.60±0.16 (505)	-	33
Xbred	Australia	REMLS	-	-	0.52±0.13 (1188)	34
ZX	Austrlia	REMLA	-	-	0.78 (1267)	35
ZX	Australia	REMLS	-	-	0.57 (1505)	36

Breeds: HEF, Hereford; ANG, Angus; RANG, Red Angus; SIM, Simmental; CHA, Charolais; SGT, Santa Gertrudis; LIM, Limousin; BSHH, Beef Shorthorn; SDV, South Devon; BSxZ, Brown Swiss cross Zebu; HxZ, Holstein cross Zebu; BA, Blond d'Aquitaine; SHH, Shorthorn; GHEF, Grade Hereford; SBP, a Synthetic beef cattle population with 35.7% Angus,34.7% Charolais,21.7% Galloway,4.5% Brown Swiss and 3.4% others(in 1978); SBP1, a Synthetic beef cattle population with approximately 33% Charolais,33% Angus and 20% Galloway breeding with small

contributions from other beef breeds ; Xbred, Cross bred consisting of 1/2 or 3/4 Brahman and 1/2,3/4,7/8,or 15/16 Sahiwal crosses with Beef Shorthorn; ZX,Zebu cross.

Methods: rPHS, correlation between paternal half-sibs; bOD, regression of offspring on dam; bOM, regression of offspring on mid parent cumulative selection differential; rFS, correlation between full-sibs; bOS, regression of offspring on sire; REMLS, restricted maximum likelihood (sire model); bOD/S, intra-sire regression of offspring on dam; bSS, regression of son on sire; REMLA, restricted maximum likelihood (multivariate animal model).

References:1, Knapp and Clark(1950); 2, Gregory et al.(1950); 3, Shelby et al.(1955); 4, Lasley et al.(1961); 5, Swiger (1961); 6, Shelby et al.(1963); 7, Brown and Galvez(1969); 8, Koch et al.(1973); 9, Pabst et al.(1977); 10, Koch (1978); 11, Nelson and Kress (1979); 12, Buchanan et al.(1982); 13, Sharma et al.(1985); 14, Wilson et al. (1986); 15, Cantet et al. (1988);16, Knights et al.(1984); 17, Alenda and Martin (1987); 18, Winder et al.(1990); 19, Burfening et al.(1978a); 20, Burfening et al.(1978b); 21, Kemp et al.(1988); 22, Willis et al.(1972); 23, Renand (1985); 24, Johnston et al.(1992a); 25, Aaron et al.(1987); 26, Massey and Benyshek (1981); 27, Fahmy and Lalande(1973); 28, Anderson et al.(1974); 29, Iloeje(1986); 30, Bourdon and Brinks(1982); 31, Smith et al.(1989); 32,Swiger et al.(1962); 33, Arthur and Makarechian(1992); 34, Robinson and Rourke (1992); 35, Mackinnon et al. (1991); 36, Mackinnon and Meyer (1992)

Figures in parentheses indicate number of observations.

TABLE 2.2 Heritability estimates for weaning weight

Breed	Country	Method	Estimate			Reference
			Male	Female	Combined	
HEF	USA	rPHS	0.28 *(880)	-	-	1
HEF	USA	rPHS	-	-	0.26 (270)	2
HEF	USA	rPHS	-	-	0.52 (69)	2
HEF	USA	rPHS	0.23 *(635)	-	-	3
HEF	USA	rPHS	0.28±0.32 (329)	0.57±0.41 (332)	-	4
HEF	USA	rPHS	0.11 (414)	-	-	5
HEF	USA	rPHS	-	0.25±0.11 (748)	-	6
HEF	USA	rPHS	0.08 *(499)	0.31 (420)	0.17 (919)	7
HEF	USA	rPHS	0.24 *(616)	-	-	8
HEF	USA	rPHS	0.33±0.08 (1915)	-	-	9
HEF	USA	rPHS	-	-	0.43 (1648)	10
HEF	USA	rPHS	0.15±0.07 (1769)	0.25±0.10 (1693)	-	11
HEF	UK	rPHS	-	-	0.38±0.06 (4439)	12
HEF	USA	rPHS	-	0.18 (377)	-	13
HEF	USA	bOM	-	0.12 (377)	-	13
HEF	USA	rPHS	0.43±0.09 (1379)	-	-	14
HEF	Canada	ML	0.18	0.24	-	15
HEF	USA	rPHS	0.23±0.02	0.18±0.01	-	16
HEF	USA	rPHS	0.15±0.17 (578)	-	-	17

HEF	Canada	rPHS	0.14 (764)	-	-	18
HEF	USA	rPHS	-	-	0.13 (46618)	19
HEF	USA	rPHS	-	-	0.28 (4423)	20
HEF	USA	rFS	-	-	0.88 (976)	20
HEF	USA	bOD	-	-	0.28	20
HEF	USA	bOS	-	-	0.06	20
HEF	USA	REMLS	0.12±0.12 (824)	-	-	21
ANG	USA	rPHS	0.32±0.16 (436)	-	-	9
ANG	USA	rPHS	-	-	0.47 (3190)	10
ANG	USA	rPHS	0.37±0.09 (1101)	0.21±0.08 (1012)	0.35±0.06 (2113)	14
ANG	Canada	ML	0.30	0.40	-	15
ANG	USA	REMLS	0.46±0.05 (717)	-	-	22
ANG	USA	rPHS	-	-	0.16 (35227)	19
ANG	USA	rPHS	0.30±0.08	0.21±0.07	-	23
AANG	UK	rPHS	-	-	0.39±0.10 (1482)	12
RANG	USA	rPHS	-	-	0.39±0.02 (41184)	24
SIM	USA	rPHS	-	-	0.28±0.04 (5578)	25
SIM	USA	rPHS	0.24±0.05	0.21±0.03	0.22±0.02 (17297)	26
SIM	Canada	ML	0.31	0.40	-	15
CHA	Canada	ML	0.23	0.30	-	15
CHA	France	rPHS	0.18±0.09 (699)	-	-	27
CHA	Canada	REMLS	-	-	0.09 (1419)	28
SGT	USA	rPHS	0.30±0.11 (939)	0.45±0.12 (955)	0.42±0.08 (1894)	29

LIM	Canada	ML	0.12	0.15	-	15
LIM	USA	rPHS	0.06±0.02	0.09±0.02	0.08±0.01 (197000)	30
SSH	Canada	ML	0.26	0.33	-	15
BSHH	Canada	bOD/S	-	-	0.13±0.11 (892)	31
BSHH	Canada	rPHS	0.47±0.20 (327)	-	-	32
BSHH	Canada	bSS	0.34±0.22	-	-	32
DEV	UK	rPHS	-	-	0.47±0.10 (1736)	12
SDV	Nigeria	rPHS	-	-	0.21±0.01 (23708)	33
SSX	UK	rPHS	-	-	0.29±0.05 (1640)	12
GHEF	USA	rPHS	0.09 *(313)	-	-	34
GHEF	USA	bOD	0.84±0.23 *(151)	-	-	34
GHEF	USA	rPHS	0.54 *(256)	-	-	34
GHEF	USA	bOD	-0.13±0.24 *(120)	-	-	34
GHEF	USA	rPHS	0.40 (679)	-	-	35
Zebu	Nigeria	rPHS	-	-	0.31±0.01 (31488)	33
BRH	Australia	REMLS	-	-	0.35±0.11 (2052)	36
BRH	Australia	REMLS	-	-	0.64±0.18 (1166)	36
Xbred	Australia	REMLS	-	-	0.33±0.11 (1188)	36
ZX	Australia	REMLA	-	-	0.56 (1267)	37
ZX	Australia	REMLS	-	-	0.21(1505)	38
HEF, ANG and RANG	USA	rPHS	0.63±0.08	0.69±0.10	-	39

HEF, ANG and RANG	USA	rPHS	-	0.14±0.06 (779)	-	40
BA, CHA and LIM	France	rPHS	0.21±0.05 (3098)	-	-	27
ANG and SSH	USA	rPHS	-	0.00±0.06 (647)	-	41
HEF and GHEF	USA	rPHS	-	0.20±0.06 (2092)	-	41
HEF and AANG	Canada	rPHS	-	-	0.32 (84021)	42
SBP	Canada	rPHS	0.25 (1313)	-	-	18
SBP1	Canada	rPHS	-	0.20±0.13 (505)	-	43

Breeds: HEF, Hereford; ANG, Angus; AANG, Aberdeen Angus; RANG, Red Angus; SIM, Simmental; CHA, Charolais; SGT, Santa Gertrudis; LIM, Limousin; SHH, Shorthorn; BSHH, Beef Shorthorn; DEV, Devon; SDV, South Devon; SSX, Sussex; GHEF, Grade Hereford; BRH, Brahman; Xbred, Cross-bred; Zx, Zebu cross; BA, Blonde Aquitaine; SBP, Synthetic beef cattle population with 35.7% Angus,34.7% Charolais,21.7% Galloway 4.5% Brown Swiss and 3.4% others (in 1978); SBP1, Synthetic beef cattle population with approximately 33% Charolais, 33% Angus and 20% Galloway breeding with small contributions from other beef breeds.

Methods: rPHS, correlation between paternal half-sibs; bOM, regression of offspring on mid parent cumulative selection differential; ML, multi-trait maximum likelihood; rFS, correlation between full-sibs; bOD, regression of offspring on dam; bOS, regression of offspring on sire; REMLS, restricted maximum likelihood (sire model); bOD/S, Intra-sire regression of offspring on dam; bSS, regression of son on sire; REMLA, restricted maximum likelihood (multivariate animal model).

References:1, Knapp and Clark(1950); 2, Gregory et al.(1950); 3, Shelby et al.(1955); 4, Pahnish et al.(1961); 5, Lasley et al. 1961); 6, Swiger(1961); 7, Blackwell et al.(1962); 8, Shelby et al.(1963); 9, Minyard and Dinkel(1965); 10, Cunningham and Henderson (1965a); 11, Koch et al.(1973); 12, Pabst et al.(1977); 13, Koch(1978); 14, Nelson

and Kress(1979); 15, Schaeffer and Wilton(1981); 16, Buchanan et al ,(1982); 17, Neely et al.(1982); 18, Sharma et al. , (1985); 19, Wilson et al.(1986); 20, Cantet et al.(1988); 21, Lamb et al.(1990); 22, Knights et al.(1984); 23, Alenda and Martin (1987); 24,Winder et al. (1990); 25, Burfening et al.(1978a); 26, Burfening et al.(1978b); 27, Renand(1985); 28, Johnston et al.(1992a); 29, Aaron et al.(1987); 30, Massey and Benyshek(1981); 31, Fahmy and Lalande (1973);32, Anderson et al.(1974); 33, Iloeje(1986); 34, Rollins and Wagnon (1956); 35, Dinkel and Busch(1973); 36, Robinson and Rourke(1992); 37, Mackinnon et al.(1991); 38, Mackinnon and Meyer(1992); 39, Bourdon and Brinks(1982); 40, Smith et al.(1989); 41, Swiger et al.(1962); 42, Kennedy and Henderson(1975a); 43, Arthur and Makarechian(1992).

Figures in parentheses indicate number of observations.

* Steers

TABLE 2.3 Heritability estimates for yearling weight

Breed	Country	Method	Estimate			Reference
			Male	Female	Combined	
HEF	USA	rPHS	0.10 *(499)	0.71 (420)	0.34 (919)	1
HEF	UK	rPHS	-	-	0.27±0.07 (1760)	2
HEF	USA	rPHS	-	0.33 (377)	-	3
HEF	USA	bOM	-	0.43 (377)	-	3
HEF	USA	rPHS	0.49±0.28 (695)	-	-	4
HEF	Canada	ML	0.18	0.36	-	5
HEF	USA	rPHS	0.23±0.02	0.37±0.03	-	6
HEF	USA	rPHS	0.33±0.19 (578)	-	-	7
HEF	Canada	rPHS	0.24 (414)	-	-	8
HEF	New Zealand	REMLS	-	-	0.17±0.06 (2414)	9
ANG	Canada	ML	0.21	0.52	-	5
ANG	USA	REMLS	0.49±0.05 (717)	-	-	10
ANG	USA	rPHS	0.36±0.08	0.18±0.07	-	11
RANG	USA	rPHS	-	-	0.40±0.02 (41184)	12
SIM	Canada	ML	0.19	0.44	-	5
CHA	Canada	ML	0.19	0.44	-	5
CHA	France	rPHS	0.32±0.12 (699)	-	-	13
CHA	Canada	REMLS	-	-	0.16 (1418)	14
LIM	USA	rPHS	0.13±0.05	0.16±0.03	0.14±0.02	15

LIM	Canada	ML	0.08	0.26	-	5
SHH	Canada	ML	0.15	0.36	-	5
BSHH	Canada	rPHS	0.04±0.16 (327)	-	-	16
BSHH	Canada	bSS	0.47±0.23	-	-	16
SDV	Nigeria	rPHS	-	-	0.33±0.01 (23708)	17
Zebu	Nigeria	rPHS	-	-	0.37±0.01 (31488)	17
BRH	Australia	REMLS	-	-	0.30±0.11 (1052)	18
XBred	Australia	REMLS	-	-	0.18±0.08 (1170)	18
HEF and AANG	Canada	rPHS	-	-	0.48 (84021)	19
HEF, ANG and RANG	USA	rPHS	0.73±0.11	0.66±0.10	-	20
HEF, ANG and RANG	USA	rPHS	-	0.29±0.08 (779)	-	21
SBP	Canada	rPHS	0.41 (660)	-	-	8
SBP1	Canada	rPHS	-	0.44+0.15 (505)	-	22
ZX	Australia	REMLA	-	-	0.48 (1267)	23
ZX	Australia	REMLS	-	-	0.29 (1505)	24

Breeds: HEF, Hereford; ANG, Angus; RANG, Red Angus; SIM, Simmental; CHA, Charolais; LIM, Limousin; SHH, Shorthorn; BSHH, Beef Shorthorn; SDV, South Devon; BRH, Brahman; XBred, Cross-bred consisting of 1/2 or 3/4 Brahman and 1/2, 3/4, 7/8 or 15/16 Sahiwal crosses with Beef Shorthorn; AANG, Aberdeen Angus; SBP, Synthetic beef cattle population with 35.7% Angus,34.7% Charolais,21.7% Galloway,4.5% Brown Swiss,3.4% others

(in1978); SBP1, a synthetic beef cattle population with approximately 33% Charolais,33% Angus and 20% Galloway breeding with small contributions from other beef breeds; ZX, Zebu cross.

Methods: rPHS, correlation between paternal half-sibs; bOM, regression of offspring on mid parent cumulative selection differential; ML, multiple trait maximum likelihood; REMLS, restricted maximum likelihood (sire model); bSS, regression of son on sire; REMLA, restricted maximum likelihood (multivariate animal model).

References:1, Blackwell et al.(1962); 2, Pabst et al.(1977); 3, Koch(1978); 4, Mavrogenis et al.(1978); 5, Schaeffer and Wilton (1981); 6, Buchanan et al.(1982); 7, Neely et al.(1982); 8, Sharma et al.(1985); 9, Morris et al.(1992); 10, Knights et al. (1984); 11, Alenda and Martin (1987); 12, Winder et al.(1990); 13, Renand and Gaillard(1982); 14, Johnston et al.(1992a); 15, Massey and Benyshek(1981); 16, Anderson et al.(1974); 17, Iloeje (1986); 18, Robinson and Rourke(1992); 19, Kennedy and Henderson (1975a); 20, Bourdon and Brinks(1982); 21, Smith et al.(1989); 22, Arthur and Makarechian (1992); 23, Mackinnon et al.(1991); 24, Mackinnon and Meyer(1992).

Figures in parentheses indicate number of observations.

* steers

TABLE 2.4 Heritability estimates for ultrasonic backfat depth and muscling score

Breed	Country	Method	Estimate			Reference
			Male	Female	Combined	
a) Ultrasonic backfat depth						
HEF	USA	rPHS	0.21±0.23 (695)	-	-	1
HEF	USA	rPHS	0.28±0.18 (578)	-	-	2
HEF	USA	REMLS	0.24±0.14 (824)	-	-	3
HEF	USA	REMLS	-	-	0.26 (3482)	4
HEF	Australia	REMLA	-	-	0.46 (1960)	5
HEF	Australia	REMLA	-	-	0.22 (1497)	5
PHEF	Australia	REMLA	-	-	0.20 (2047)	5
GHEF	USA	rPHS	0.57 *(679)	-	-	6
ANG	Australia	REMLA	-	-	0.42 (1910)	5
ANG	Australia	REMLA	-	-	0.41 (1818)	5
HEF, ANG and PHEF	Australia	REMLA	-	-	0.34 (9232)	5
b) Muscling score						
HEF	USA	rPHS	*0.40 (499)	0.34 (420)	-	7
HEF	Hawaii	rPHS	0.12±0.15	0.57±0.16	0.41±0.11	8
HEF	USA	rPHS	-	0.27 (377)	-	9
HEF	USA	rPHS	0.24±0.02	0.30±0.03	-	10
HEF	Australia	REMLA	-	-	0.14 (1960)	5

GHEF	USA	rPHS	0.25 *(679)	-	-	6
ANG	Hawaii	rPHS	0.61±0.53	1.71±0.83	1.32±0.50	8
ANG	Australia	REMLA	-	-	0.17 (1910)	5
CHA	France	rPHS	0.21±0.10 (699)	-	-	11
CHA, BA and LIM	France	rPHS	0.28±0.05 (3098)	-	-	11
HEF and ANG	Hawaii	rPHS	-	-	0.56±0.11 (1759)	8

Breeds: HEF, Hereford; PHEF, Polled Hereford; GHEF, Grade Hereford; ANG, Angus; CHA, Charolais; BA,Blond d' Aquitaine; LIM, Limousin.

Methods: rPHS,correlation between paternal half-sibs ; REMLS, restricted maximum likelihood (sire model); REMLA, restricted maximum likelihood (animal model).

References:1, Mavrogenis et al.(1978); 2, Neely et al.(1982); 3, Lamb et al.(1990); 4, Arnold et al.(1991); 5, Robinson et al. (1992); 6, Dinkel and Busch(1973); 7, Blackwell et al.(1962); 8, Francoise et al.(1973); 9, Koch(1978); 10, Buchanan et al. (1982); 11, Renand(1985).

Figures in parenthesis indicate number of observations.

* Steers

(ii) the absence of selection between sires, (iii) the absence of environmental correlations between half-sibs, and (iv) a large number of progeny per sire. Moreover, the assumptions of random mating, absence of epistatic effects and no covariance between genotype and environment must hold. The major advantage of using paternal half-sib correlation to estimate h^2 is that this value contains only the additive plus a negligible fraction of the epistatic portion of the genotypic variance. In this method the intraclass correlation is multiplied by 4, since the average relationship among half-sibs is one-fourth. This method is limited by the fact that errors due to sampling or incorrect estimation of environmental influences are multiplied by 4.

With the availability of increased computer power the use of restricted maximum likelihood (Patterson and Thompson, 1971) and animal models has become a standard practice in the analyses of the animal breeding data throughout the world. This method has some unique attributes which have made it the method of choice. For example, it accounts for the loss in degrees of freedom due to fixed effects in the model, it is an iterative procedure well suited for use with mixed model equations; it eliminates the bias due to selection and it takes into account all the relationships present in the pedigree.

The estimates of h^2 for birth weight in various breeds are given in TABLE 2.1. They range from 0.09 in Holstein x Zebu to 1.00 in Hereford cattle. The average estimates for males and females are 0.46 and 0.39, respectively, 0.24 being the average across sexes (TABLE 2.5).

The h^2 estimates for weaning weight are presented in TABLE 2.2. The average values of h^2 estimated for weaning weight are 0.26 in males, 0.23 in females, 0.27 in steers and 0.20 across sexes. Wide ranges were observed for h^2 estimates from 0.06 to 0.63 in males, from 0.00 to 0.69 in

TABLE 2.5 Average heritability and repeatability estimates for various performance traits

Sexes		Birth weight	Weaning weight	Yearling weight	Backfat depth	Muscling score
(i) Heritability estimates (For traits of calf):						
Males	No.of studies	14	16	9	3	2
	Average	0.46	0.26	0.49	0.24	0.24
	Range	0.17 to 0.72	0.06 to 0.63	0.04 to 0.73	0.21 to 0.28	0.12 to 0.60
Females	No.of studies	10	12	7	-	2
	Average	0.39	0.23	0.48	-	0.31
	Range	0.17 to 0.60	0.00 to 0.69	0.16 to 0.71	-	0.27 to 1.71
Steers	No.of studies	-	9	1	1	2
	Average	-	0.27	0.10	0.57	0.31
	Range	-	-0.13 to 0.84	-	-	0.25 to 0.40
Combined	No.of studies	27	29	12	7	3
	Average	0.24	0.20	0.41	0.33	0.28
	Range	0.09 to 1.00	0.06 to 0.88	0.14 to 0.48	0.20 to 0.46	0.14 to 1.32
(ii) Repeatability estimates (For traits of dam):						
Males	No.of studies	3	8	1	-	-
	Average	0.21	0.44	0.21	-	-
	Range	0.14 to 0.26	0.42 to 0.52	-	-	-
Females	No.of studies	1	5	1	-	-
	Average	0.29	0.27	0.48	-	-
	Range	-	0.25 to 0.50	-	-	-
Steers	No.of studies	-	4	-	-	-
	Average	-	0.24	-	-	-
	Range	-	0.19 to 0.51	-	-	-
Combined	No.of studies	5	10	-	-	-
	Average	0.23	0.23	-	-	-
	Range	-0.03 to 0.41	0.21 to 0.52	-	-	-

females and from -0.13 to 0.84 in steers. Small and negative estimates of sire component h^2 (Rollins and Wagnon, 1956; Swiger et al.,1962 Blackwell et al.,1962 and Massey and Benyshek,1981) may be attributed to small number of progeny per sire group, sampling error or genotype-environmental interaction besides other factors. Gill and Jensen (1968) investigated the probability of obtaining negative estimates of h^2.They demonstrated that if the true h^2 is relatively low (0.10), at least 800 observations are necessary for a 95% chance of obtaining a non-negative estimate from the sire component of variance, and that more than 800 observations are needed if information per sire is limited to fewer than 30-40 progeny. A negative environmental correlation between preweaning growth of the female and her subsequent maternal ability has been reported by Mangus and Brinks (1971) and Koch (1972). Such a correlation would be expected to lower the offspring-dam regression estimates of h^2 .

The h^2 estimates for yearling weight are given in TABLE 2.3. They range between 0.04 and 0.73 in males, between 0.16 and 0.71 in females and between 0.14 and 0.48 across sexes. The corresponding average values are 0.49, 0.48 and 0.41 (TABLE 2.5). As these estimates are high, it seems that the trait will respond to selection.

The estimates of h^2 for muscling score and backfat depth are given in TABLE 2.4. Average estimates of h^2 for backfat depth are 0.24 in males, 0.33 across sexes. The only estimate available for steer data is high (0.57). In general ultrasonic backfat depth seems moderate to highly heritable. Muscling score h^2 estimates vary very widely from 0.12 to 0.60 in males, from 0.27 to 1.71 in females, from 0.25 to 0.40 in steers and from 0.14 to 1.32 across sexes. This wide variation may be partly attributed to the subjective nature of muscling score and to differences in age at measurement in different studies. Unrealistically high estimates of h^2 for

muscling score (1.71, 1.32) have been reported by Francoise et al.,(1973) from the analysis of data on Angus cattle in Hawaii using paternal half-sib correlation technique.

2.3 Genetic parameter estimates due to maternal effects

It has been reported by many workers (chapter 1) that growth traits in beef cattle are affected not only by direct genetic effects but also by the maternal genetic and maternal environmental effects, besides other factors. Various workers have estimated and reviewed genetic parameter estimates due to maternal effects on growth traits in beef cattle (for example, Baker,1980 and Meyer,1992). The genetic parameter estimates due to maternal effects on birth weight are given in TABLE 2.6. The heritability estimate due to direct additive genetic effects (h^2_A, direct heritability) on birth weight range between 0.14 and 0.61 in different breeds, 0.30 being the average of 43 studies (TABLE 2.9). The heritability estimates due to maternal additive genetic effects (h^2_M, maternal heritability) on birth weight vary from 0.03 to 0.82, the average being 0.10. The correlation between direct additive genetic and maternal additive genetic effects (r_{AM}) shows a wide variation (from -1.05 to 0.55). The average r_{AM} is large and negative (-0.35), indicating antagonism between the genes for prenatal growth and the genes conditioning the intra-uterine environment for heavier weights at birth. Such an antagonism would be a balanced mechanism to maintain birth weights in intermediate ranges (Brown and Galvez, 1969). The maternal permanent environmental variance as a proportion of the phenotypic variance (c^2) averages 0.03 (TABLE 2.9). The covariance between the direct additive genetic and maternal additive genetic effects as a proportion of the phenotypic variance (c_{AM}) ranges from -0.24 to 0.05. The heritability estimates for the total

TABLE 2.6 Genetic parameter estimates due to maternal effects on birth weight

Breed	Country	No.	Model	Estimate						Reference
				h_A^2	h_M^2	r_{AM}	c^2	c_{AM}	h_T^2	
HEF	USA	789	-	0.56	0.30	-0.58	-	-0.24	0.36	1
HEF	USA	1012[A]	-	0.36	0.82	-0.51	-	-	0.35	2
HEF	USA	4423	-	0.18	0.21	-1.05	-	-0.21	-0.02	3
HEF	Canada	175282	SMGS	0.39	0.13	-0.39	-	-	0.32	4
HEF	USA	-	AMMP	0.43	0.12	0.07	0.02	0.02	0.51	5
HEF	USA	2039	SDSMGS	0.58	0.22	-0.13	0.03	-0.05	0.62	6
HEF	Australia	5488	AM	0.56	-	-	-	-	0.56	7
HEF	Australia	5488	AMP	0.49	-	-	0.10	-	0.49	7
HEF	Australia	5488	AMM	0.39	0.14	-	-	-	0.46	7
HEF	Australia	5488	AMM1	0.38	0.14	0.05	-	0.01	0.47	7
HEF	Australia	5488	AMMP1	0.42	0.09	-	0.05	-	0.46	7
HEF	Australia	5488	AMMP	0.41	0.08	0.04	0.05	0.01	0.46	7
HEF	USA	2039	SDSMGS	0.58	0.22	-0.13	0.03	-0.05	0.62	8
PHEF	Australia	3414	*AMMP1	0.43	0.10	-	0.09	-	0.48	9
ANG	USA	932	-	0.14	0.25	-0.39	-	-0.07	0.17	1
ANG	Canada	50767	SMGS	0.37	0.13	-0.34	-	-	0.32	4
ANG	USA	2514	SDSMGS	0.42	0.22	-0.12	-0.38	-0.04	0.47	6
ANG	Australia	4036	AM	0.52	-	-	-	-	0.52	7
ANG	Australia	4036	AMP	0.47	-	-	0.08	-	0.47	7

ANG	Australia	4036	AMM	0.40	0.13	-	-	-	0.46	7
ANG	Australia	4036	AMM1	0.34	0.10	0.27	-	0.05	0.47	7
ANG	Australia	4036	AMMP1	0.42	0.08	-	0.04	-	0.46	7
ANG	Australia	4036	AMMP	0.36	0.07	0.29	0.03	0.05	0.46	7
ANG	USA	2514	SDSMGS	0.42	0.22	-0.12	-0.38	-0.04	0.47	8
ANG	Australia	4036	*AMMP1	0.44	0.08	-	0.03	-	0.48	10
SIM	USA	4196	-	0.21	0.11	-0.24	-	-	0.21	11
SIM	USA	497409	-	0.16	0.06	-0.44	-	-	0.13	12
SIM	Canada	60807	SMGS	0.34	0.20	-0.22	-	-	0.36	4
SIM	USA	296659	SMGS	0.44	0.12	-0.38	-	-0.09	0.37	13
SIM	Australia	58618	AMM1	0.33	0.07	-0.04	-	-0.01	0.36	14
SHH	Canada	15839	SMGS	0.27	0.20	0.55	-	-	0.56	4
CHA	Canada	31252	SMGS	0.42	0.17	-0.39	-	-	0.35	4
LIM	USA	78088	SDSMGS	0.22	0.05	-0.16	0.05	-0.02	0.22	15
BRG	USA	20750	SDSMGS	0.25	0.13	-0.12	0.00	-0.02	0.28	15
BRG	USA	32215	MTPEA	0.28	0.12	-0.52	-	-	0.20	16
SGT	USA	10768	MTPEA	0.34	0.26	-0.58	-	-	0.21	16
BM	USA	2388	MTPEA	0.22	0.55	-0.53	-	-	0.22	16
BRH	USA	5459	MTPEA	0.37	0.18	-0.15	-	-	0.40	16
AX	Australia	1406	SDSMGS	0.47	0.05	-	0.07	-	0.49	17
HSX	Australia	1346	SDSMGS	0.23	0.03	-	0.18	-	0.24	17
BRHX	Australia	1081	SDSMGS	0.45	0.14	-	0.00	-	0.52	17
ZX	Australia	1267	AMM1	0.61	0.11	0.01	-	0.02	0.68	18

Xbred	Australia	1188	AM	0.58	-	-	-	-	0.58	19
Xbred	Australia	1188	AMM	0.45	0.10	-	-	-	0.55	19
WOKA	Australia	3769	*AMMP1	0.52	0.06	-	0.04	-	0.55	9

Breeds:HEF, Hereford; PHEF, Polled Hereford; ANG, Angus; SIM, Simmental; SHH, Shorthorn; CHA, Charolais; LIM, Limousin; BRG, Brangus; SGT, Santa Gertrudis; BM, Beefmaster; BRH, Brahman ; AX, Africander cross; HSX, Hereford Shorthorn cross; BRHX, Brahman cross; ZX, Zebu cross; Xbred, Crossbred consisting of 1/2,3/4 Brahman and 1/2, 3/4,7/8 or 15/16 Sahiwal crosses with Beef Shorthorn; WOKA, Wokalups,a synthetic breed formed by mating of Charolais X Brahman bulls with Friesian x Angus or Hereford cows.

Models: SMGS, sire-maternal grandsire model; AMMP, animal model with permanent environmental dam effect and maternal genetic effect and $\sigma_{AM}\neq 0$; SDSMGS, sire-dam model and sire-maternal grandsire model; AM, simple animal model; AMP, animal model with permanent environmental dam effect; AMM, animal model with maternal genetic effect and $\sigma_{AM}=0$; AMM1, animal model with maternal genetic effect and $\sigma_{AM}\neq 0$; AMMP1, animal model with permanent environmental dam effect and maternal genetic effect and $\sigma_{AM}=0$; MTPEA, multiple-trait pseudo expectation approach.

References:1, Brown and Galvez(1969); 2, Nelson et al.(1984); 3, Cantet et al.(1988); 4, Trus and Wilton (1988); 5, Koch, (1989) cited by Meyer(1992); 6, Brown et al . (1990); 7, Meyer(1992); 8, Johnson et al.(1992); 9, Meyer et al. (1992a); 10, Meyer et al. (1992b); 11, Burfenning et al.(1981); 12, Quaas et al.(1985); 13, Garrick et al.(1989); 14, Swalve(1992); 15, Bertrand and Benyshek(1987); 16, Kriese et al. (1991); 17, Hetzel et al.(1990); 18, Mackinnon et al. (1991); 19, Robinson and Rourke (1992).

Symbols used: h^2_A, direct heritability, i.e. heritability of the direct additive genetic effects; h^2_M, maternal heritability, i.e. heritability of the maternal additive genetic effects; r_{AM}, correlation between direct additive genetic effects and maternal additive genetic effects; c^2, maternal permanent environmental effects as a proportion of the phenotypic variance; c_{AM}, covariance between direct additive genetic effects and maternal additive genetic effects as a

proportion of the phenotypic variance; h^2_T, total heritability, i.e. heritability of the total additive genetic effects as proposed by Willham (1972).

A ; males, all others combined.

* bivariate

additive effects (h^2_T, total heritability, after Willham, 1972) on birth weight range from -0.02 to 0.68 in different breeds.

The genetic parameter estimates due to maternal effects on weaning weight are given in TABLE 2.7. The average h^2_A, h^2_M, and h^2_T, are 0.22, 0.13 and 0.23 respectively. The r_{AM} is negative and small (Table 2.9). The genetic parameter and environmental estimates due to maternal effects on yearling weight are presented in TABLE 2.8. Values of h^2_A, h^2_M, and h^2_T show wide variation (0.12-0.50, 0.02-0.20 and 0.02-0.50, respectively). The r_{AM} value is negative and moderate in magnitude.

TABLE 2.6 on the genetic parameter estimates due to maternal effects on birth weight contains 12 references (6 on Hereford and 6 on Angus cattle) from a study conducted by Meyer(1992) and TABLES 2.7 and 2.8 on genetic parameters estimates due to maternal effects on weaning weight and yearling weight, respectively contain 18 references (6 on Hereford, 6 on Angus and 6 on Zebu cross animals) from this study. She tries to explain the effect of the inclusion of different random terms on the estimates of (co)variance components and the resulting genetic parameters. Meyer 's (1992) study appears to be the first of its kind in the available literature which attempted to demonstrate the effect of various methods of estimation (using REML individual animal model).

The average estimates of genetic parameters due to maternal effects on weight traits are lower than those presented by Baker (1980) from a review of the literature concerning beef traits. For example, the h^2_A, h^2_M, h^2_T and r_{AM} values as reported by Baker (1980) are 0.40, 0.19, 0.34 and –0.42, respectively for birth weight and 0.30, 0.52, 0.25 and –0.72 for weaning weight. The weighted means of h^2_A and h^2_M for these three weight traits reported by Koots et al.(1994) from a recent review of the literature comprising results in addition to those reported here are almost the same.

TABLE 2.7 Genetic parameter estimates due to maternal effects on weaning weight

Breed	Country	No.	Model	Estimate						Reference
				h^2_A	h^2_M	r_{AM}	c^2	c_{AM}	h^2_T	
HEF	USA	-	-	0.18	0.24	0.25	-	-	0.38	1
HEF	USA	4423	-	0.32	0.27	-0.57	-	-0.17	0.20	2
HEF	USA	-	AMMP	0.16	0.19	-0.20	0.26	-0.03	0.20	3
HEF	USA	1835	SDSMGS	0.66	0.43	-0.08	-0.22	-0.04	0.81	4
HEF	Australia	7003	AM	0.26	-	-	-	-	0.26	5
HEF	Australia	7003	AMP	0.10	-	-	0.29	-	0.10	5
HEF	Australia	7003	AMM	0.07	0.34	-	-	-	0.24	5
HEF	Australia	7003	AMM1	0.14	0.46	-0.59	-	-0.15	0.14	5
HEF	Australia	7003	AMMP1	0.09	0.07	-	0.24	-	0.12	5
HEF	Australia	7003	AMMP	0.14	0.13	-0.59	0.23	-0.08	0.09	5
HEF	USA	1835	SDSMGS	0.66	0.43	-0.08	-0.22	-0.04	0.81	6
HEF	USA	-	SDSMGS	0.24	0.24	-0.28	0.08	-0.06	0.25	7
PHEF	USA	-	SDSMGS	0.23	0.30	-0.27	0.03	-0.07	0.26	7
PHEF	Australia	3088	*AMMP1	0.19	0.13	-	0.20	-	0.26	8
CHEF	USA	-	SDSMGS	0.22	0.33	-0.26	0.03	-0.07	0.28	7
ANG	USA	-	-	0.24	0.18	0.15	-	-	0.38	1
ANG	USA	2309	SDSMGS	0.63	0.16	-0.36	-0.31	-0.11	0.54	4
ANG	Australia	3465	AM	0.44	-	-	-	-	0.44	5
ANG	Australia	3465	AMP	0.32	-	-	0.13	-	0.32	5

ANG	Australia	3465	AMM	0.22	0.20	-	-	-	0.32	5
ANG	Australia	3465	AMM1	0.19	0.18	0.20	-	0.04	0.33	5
ANG	Australia	3465	AMMP1	0.23	0.16	-	0.04	-	0.31	5
ANG	Australia	3465	AMMP	0.20	0.14	0.22	0.04	0.04	0.32	5
ANG	USA	2309	SDSMGS	0.63	0.16	-0.36	-0.31	-0.11	0.54	6
ANG	Australia	3465	*AMMP1	0.26	0.11	-	0.05	-	0.32	9
RANG	USA	41184	SMGS	0.40	0.10	-	-	-	0.45	10
SIM	USA	768419	SMGS	0.12	0.08	-0.04	-	-	0.15	11
SIM	Australia	15605	SMGS	0.10	0.13	0.04	-	0.01	0.17	12
SIM	USA	114899	SMGS	0.12	0.09	0.16	0.07	0.02	0.19	13
SIM	USA	425085	SMGS	0.36	0.19	-0.32	-	-0.08	0.33	14
SIM	UK	8206	AM	0.30	-	-	-	-	0.30	15
SIM	UK	8897	AM	0.32	-	-	-	-	0.32	16
SIM	UK	8897	AMP	0.19	-	-	0.08	-	0.19	16
SIM	UK	8897	AMM	0.19	0.07	-	-	-	0.23	16
SIM	Australia	52097	AMMP	0.35	0.18	-0.39	0.08	-0.10	0.29	17
SGT	USA	23180	MTPEA	0.25	0.18	-0.43	-	-	0.20	18
LIM	USA	53494	SDSMGS	0.16	0.15	-0.30	0.06	-0.05	0.17	19
BRG	USA	46661	SDSMGS	0.28	0.20	-0.29	0.04	-0.07	0.28	19
BRG	USA	58932	MTPEA	0.21	0.15	-0.23	-	-	0.22	18
BM	USA	7211	MTPEA	0.21	0.21	-0.06	-	-	0.30	18
SNP	USA	4634	SDSMGS	0.21	0.47	-0.57	-0.39	-0.18	0.18	20
BRH	USA	12559	MTPEA	0.23	0.16	0.15	-	-	0.60	18

BRH	Australia	2052	AM	0.37	-	-	-	-	0.37	21
BRH	Australia	2052	AMM	0.35	0.04	-	-	-	0.37	21
BRH	Australia	1166	AM	0.64	-	-	-	-	0.64	21
BRH	Australia	1166	AMM	0.52	0.07	-	-	-	0.56	21
NLR	Brasil	7415	-	0.26	0.28	-0.91	-	-	0.02	22
Xbred	Australia	1188	AM	0.58	-	-	-	-	0.58	21
Xbred	Australia	1188	AMM	0.31	0.19	-	-	-	0.41	21
AX	Australia	-	SDSMGS	0.15	0.30	-	0.06	-	0.30	23
HSX	Australia	-	SDSMGS	0.20	0.12	-	0.19	-	0.25	23
BRHX	Australia	-	SDSMGS	0.12	0.08	-	0.21	-	0.16	23
BRHX	Australia	-	AMM	0.34	0.16	-	-	-	0.42	24
ZX	Australia	1267	AMM1	0.20	0.32	0.00	-	0.00	0.36	25
ZX	Australia	2842	AM	0.34	-	-	-	-	0.34	5
ZX	Australia	2842	AMP	0.27	-	-	0.23	-	0.27	5
ZX	Australia	2842	AMM	0.23	0.24	-	-	-	0.35	5
ZX	Australia	2842	AMM1	0.59	0.49	-0.74	-	-0.40	0.24	5
ZX	Australia	2842	AMMP1	0.25	0.11	-	0.14	-	0.31	5
ZX	Australia	2842	AMMP	0.58	0.36	-0.78	0.11	-0.36	0.23	5
ZX	Australia	2842	*AMMP1	0.21	0.11	-	0.17	-	0.27	9
ZX	Australia	2842	*AMMP	0.41	0.28	-0.70	0.15	-0.24	0.19	9
WOKA	Australia	3191	*AMMP1	0.31	0.06	-	0.10	-	0.34	8

Breeds: HEF,Hereford; PHEF, Polled Hereford; CHEF, Canadian Hereford; ANG, Angus; RANG, Red /Angus; SIM, Simmental; SGT, Santa Gertrudis; LIM, Limousin; BRG, Brangus; BM, Beefmaster; SNP, Senepol; BRH, Brahman;

NLR, Nelore; Xbred, Crossbred; AX, Africander cross; HSX, Hereford Shorthorn cross; BRHX, Brahman cross; ZX, Zebu cross; WOKA; Wokalups, a synthetic breed formed by mating of Charlais x Brahman bulls with Friesian x Angus or Hereford cows.

Models: AMMP, animal model with permanent environmental dam effect and maternal genetic effect and $\sigma_{AM} \neq 0$; SDSMGS, sire-dam model and sire maternal grandsire model; AM, simple animal model; AMP, animal model with a permanent environmental dam effect; AMM, animal model with maternal genetic effect and $\sigma_{AM}=0$; AMM1, animal model with maternal genetic effects and $\sigma_{AM} \neq 0$; AMMP1, animal model with permanent environmental dam effect and maternal genetic effect and $\sigma_{AM}=0$; SMGS, sire-maternal grandsire model; MTPEA, multiple trait pseudo-expectation approach.

References:1, Skaar(1985); 2, Cantet et al.(1988); 3, Koch(1989) cited by Meyer(1992); 4, Brown et al.(1990) ; 5, Meyer (1992); 6, Johnson et al. (1992); 7, Johnston et al.(1992b); 8, Meyer et al.(1992a); 9, Meyer et al.(1992b); 10, Winder et al.(1990); 11, Quaas et al.(1985); 12, Graser and Hammond(1985); 13, Wright et al.(1987); 14, Garrick et al.(1989); 15, Perez-Camara(1990); 16, Mrode and Thompson(1990); 17, Swalve(1992); 18, Kriese et al.(1991); 19, Bertrand and Benyshek (1987); 20, Wright et al.(1991); 21, Robinson and Rourke(1992); 22, Eler et al . (1992); 23, Hetzel et al.(1990); 24, Robinson (1990);25, Mackinnon et al.(1991).

See TABLE 2.6 for symbols used.

* bivariate

TABLE 2.8 Genetic parameter estimates due to maternal effects on yearling weight

Breed	Country	No.	Model	Estimate						Reference
				h_A^2	h_M^2	r_{AM}	c^2	c_{AM}	h_T^2	
HEF	Australia	1449	AM	0.21	-	-	-	-	0.21	1
HEF	Australia	1449	AMP	0.14	-	-	0.09	-	0.14	1
HEF	Australia	1449	AMM	0.12	0.10	-	-	-	0.17	1
HEF	Australia	1449	AMM1	0.15	0.14	-0.41	-	-0.06	0.14	1
HEF	Australia	1449	AMMP	0.12	0.07	-	0.04	-	0.15	1
HEF	Australia	1449	AMMP1	0.16	0.11	-0.48	0.05	-0.06	0.12	1
HEF	Australia	419	AM	0.27	-	-	-	-	0.27	2
PHEF	Australia	1229	*AMMP	0.19	0.15	-	0.08	-	0.27	3
ANG	Australia	2374	AM	0.50	-	-	-	-	0.50	1
ANG	Australia	2374	AMP	0.44	-	-	0.06	-	0.44	1
ANG	Australia	2374	AMM	0.40	0.08	-	-	-	0.44	1
ANG	Australia	2374	AMM1	0.32	0.06	0.45	-	0.06	0.44	1
ANG	Australia	2374	AMMP	0.40	0.05	-	0.03	-	0.43	1
ANG	Australia	2374	AMMP1	0.33	0.04	0.49	0.03	0.05	0.43	1
ANG	Australia	2374	*AMMP	0.41	0.02	-	0.02	-	0.42	4
SIM	UK	4461	AM	0.30	-	-	-	-	0.30	5
SIM	UK	5890	AM	0.31	-	-	-	-	0.31	6
SIM	UK	5890	AMP	0.26	-	-	0.05	-	0.26	6
SIM	UK	5890	AMM	0.27	0.03	-	-	-	0.29	6

SIM	Australia	52097	AMMP1	0.37	0.11	-0.22	0.01	-0.05	0.36	7
ZX	Australia	1267	AMM1	0.25	0.20	0.01	-	0.01	0.36	8
ZX	Australia	2480	AM	0.27	-	-	-	-	0.27	1
ZX	Australia	2480	AMP	0.22	-	-	0.10	-	0.22	1
ZX	Australia	2480	AMM	0.18	0.12	-	-	-	0.23	1
ZX	Australia	2480	AMM1	0.24	0.17	-0.38	-	-0.08	0.21	1
ZX	Australia	2480	AMMP	0.18	0.10	-	0.03	-	0.23	1
ZX	Australia	2480	AMMP1	0.25	0.14	-0.39	0.03	-0.07	0.21	1
ZX	Australia	2480	*AMMP	0.20	0.07	-	0.06	-	0.24	4
ZX	Australia	2480	*AMMP1	0.24	0.09	-0.35	0.08	-0.05	0.21	4
BRH	Australia	1052	AM	0.36	-	-	-	-	0.36	9
BRH	Australia	1052	AMM	0.30	0.06	-	-	-	0.33	9
NLR	Brasil	7415	-	0.18	0.18	-0.91	-	-	0.02	10
BRHX	Australia	-	AMM	0.21	0.12	-	-	-	0.27	11
Xbred	Australia	1170	AM	0.41	-	-	-	-	0.41	9
Xbred	Australia	1170	AMM	0.20	0.14	-	-	-	0.27	9
WOKA	Australia	1373	*AMM	0.34	0.13	-	-	-	0.41	3

Breeds: HEF, Hereford; PHEF, Polled Hereford; ANG, Angus; SIM, Simmental; ZX, Zebu cross; BRH, Brahman; NLR, Nelore; BRHX, Brahman cross; Xbred, Crossbred consisting of 1/2 or 3/4 Brahman and 1/2, 3/4,7/8 or 15/16 Sahiwal crosses with Beef Shorthorn; WOKA, Wokalups, a synthetic breed formed by mating of Charolais x Brahman bulls with Friesian x Angus or Hereford cows.

Models: AM, animal model (simple); AMP,animal model with permanent environmental dam effect; AMM animal model with maternal genetic effect and $\sigma_{AM}=0$; AMM1, animal model with maternal genetic effect and $\sigma_{AM}\neq 0$; AMMP,

animal model with permanent environmental dam effect and maternal genetic effect and $\sigma_{AM}=0$; AMMP1, animal model with permanent environmental dam effect and maternal genetic effect and $\sigma_{AM}\neq 0$.

References:1, Meyer(1992); 2, Meyer et al.(1991); 3, Meyer et al.(1992a); 4, Meyer et al.(1992b); 5, Perez-Camara (1990); 6, Mrode and Thompson (1990) ;7, Swalve(1992); 8, Mackinnon et al.(1991); 9, Robinson and Rourke (1992);10, Eler et al.(1992); 11, Robinson (1990).

See Table 2.6 for symbols used.

* bivariate

TABLE 2.9 Average genetic and environmental parameter estimates due to maternal effects on growth traits

Parameter		Birth weight	Weaning weight	Yearling weight
h^2_A	No. of studies	43	53	35
	Average	0.30	0.22	0.31
	Range	0.14 to 0.61	0.07 to 0.66	0.12 to 0.50
h^2_M	No.of studies	38	41	23
	Average	0.10	0.13	0.11
	Range	0.03 to 0.82	0.04 to 0.49	0.02 to 0.20
r_{AM}	No.of studies	27	26	10
	Average	-0.35	-0.15	-0.26
	Range	-1.05 to 0.55	-0.91 to 0.26	-0.91 to 0.49
c^2	No.of studies	18	24	15
	Average	0.03	0.07	0.03
	Range	-0.38 to 0.18	-0.39 to 0.29	0.01 to 0.10
c_{AM}	No.of studies	16	20	9
	Average	-0.06	-0.07	-0.04
	Range	-0.24 to 0.05	-0.40 to 0.04	-0.08 to 0.06
h^2_T	No.of studies	43	53	35
	Average	0.27	0.23	0.31
	Range	-0.02 to 0.68	0.02 to 0.81	0.02 to 0.50

See TABLE 2.6 for symbols used.

They observed values for h^2_A and h^2_M of 0.31, 0.14 and 0.24, 0.13 for birth weight and weaning weight, respectively while respective values of h^2_A (weighted) and h^2_M (unweighted) for yearling weight were 0.33 and 0.11, respectively. It should be noted that the weighting factor used in the present study is the number of observations while they weighted the estimates by the inverse of the sampling variance. The review by Koots et al.(1994) appeared after my review was published (Mohiuddin, 1993). They included more references but mainly unrefereed literature (in particular technical reports of various research stations). However, the main conclusions of the two reviews were similar.

There is a paucity of information concerning maternal effects on muscling score and backfat depth. The only study reported is of Robinson et al.(1992) who analysed data of 9232 Angus, Hereford and Polled Hereford cattle aged between 300 and 600 days at the time of scanning. Average maternal permanent environmental effects for ultrasonic rump and rib fat were 4% and 11%, respectively. Average maternal genetic effects were 6% for rump fat and 5% for rib fat.

The literature concerning genetic parameter estimates due to maternal effects on weight traits indicates that there should be little or no loss in genetic progress for the maternal traits when selection is applied to direct and maternal effects as total heritabilities are at least as high as direct heritabilities. The benefit over reliance on selecting for the direct effect alone could be in the reduction of per cow costs, thereby increasing production efficiency.

Maternal heritabilities were lower than direct heritabilities. This implies that weight traits were determined more by the genetic characteristics of the calf than by those of the dam. This is in line with the findings of Koots et al.(1994) in their review. They observed that

heritabilities of maternal traits (h^2_M) were lower than for the corresponding direct traits (h^2_A) and the difference between the values of h^2_A and h^2_M was significant for birth weight and weaning weight.

The average correlation between direct additive genetic and maternal additive genetic effects is negative for the three weight traits reviewed. It is highest for birth weight (–0.35), followed by yearling (–0.26) and weaning weight (–0.15). This estimate of the genetic correlation between direct and maternal effects seems to suggest that many of the same genes possess opposite effects on direct and maternal components of birth, weaning and yearling weight. It indicates a tendency for animals with superior growth genes to have inferior maternal genes and vice versa (Garrick,1990). This would suggest that genes which partition nutrients for growth of the young calf are partly incompatible with genes which partition nutrients for lactation. Garrick (1990) suggests that this negative correlation may be the result of many generations of natural selection with an intermediate optimum. Koch and Clark(1955) are of the view that if r_{AM} is negative more emphasis should be placed on selecting cows on the basis of their calf's weaning weight if selection for maternal ability is to keep pace with selection for growth response. In fact, if extreme emphasis is placed on calf gains alone, particularly on yearling gains, there could actually be a loss in genetic value for milking ability. It must be cautioned that this negative correlation between direct additive genetic and maternal additive genetic effects may be induced by environmental factors such as management and husbandry practices. If r_{AM} is zero, selection for the trait would tend to be more for the genes for growth in the offspring than for maternal influence. If it is positive, selection improves both direct genetic and maternal genetic components. However, if it is negative and high,

optimal procedure would be to select for maternal genetic effects in females and genetic values for growth in males.

A wide variation in the estimates of genetic parameters due to maternal effects on growth traits may be attributed to the method of analysis as well as other reasons. During the last decade estimates were obtained by comparisons of expected composition of variances and covariances with observed values from different types of relatives. Mainly sire-dam model and sire-maternal grandsire models were employed for this purpose. Such comparisons are biased and subject to large errors due to generally small number of relatives involved. Recent estimates have been obtained by the use of animal model with maternal effects mostly using the programmes based on software written by Meyer (1989,1991).

2.4 Repeatability Estimates

The repeatability estimates of weight traits are given in TABLE 2.10. The repeatability estimates for birth weight (trait of the cow expressed through the calf) range between –0.03 and 0.41 in various breeds, the average values being 0.21 in males, 0.29 in females and 0.23 across sexes (TABLE 2.5). A negative estimate for repeatability of birth weight was reported by Gregory et al.(1950) in Hereford cattle. The main reason for this very low estimate might be the small data set used. The average values for repeatability of birth weight (trait of the cow) are lower than the corresponding estimates of heritability for the trait (trait of the calf). It seems that genotype of the calf is more important than maternal influence in determining birth weight.

The repeatability estimates for weaning weight vary from 0.21 to 0.52 in different breeds .The average values of repeatability for male, female and combined data sets are relatively high, being of the order of 0.44, 0.27 and 0.23, respectively (TABLE 2.5). The average repeatability estimates for

TABLE 2.10 Repeatability estimates for birth, weaning and yearling weights (as traits of the dam)

Breed	Country	Method	Estimate			Reference
			Male	Female	Combined	
a) Birth weight						
HEF	USA	a	-	-	0.11-0.24 (281)	1
HEF	USA	a	-	-	-0.03 (74)	1
HEF	USA	-	-	-	0.21 (4423)	2
ANG	USA	b	0.26±0.04	0.29±0.04	-	3
BSHH	Canada	b	-	-	0.41±0.04 (892)	4
GHEF	USA	c	0.14 (620)		-	5
GHEF	USA	b	0.18 (620)		-	5
HEF, ANG and RANG	USA	b	-	-	0.22±0.02 (5068)	6
b) Weaning weight						
HEF	USA	a	0.49 (911)	-	-	7
HEF	USA	a	-	-	0.37-0.50 (270)	1
HEF	USA	a	-	-	0.43 (69)	1
HEF	USA	b	-	-	0.52 (745)	8
HEF	USA	b	0.42±0.04 (1915)	-	-	9
HEF	UK	b	-	-	0.42±0.04 (693)	10
HEF	USA	b	0.27±0.003 *(9999)	-	-	11
HEF	USA	b	-	0.50±0.04 (634)	-	12

HEF	USA	-	-	-	0.30 (4423)	2
ANG	USA	b	0.52±0.13 (436)	-	-	9
AANG	UK	b	-	-	0.39±0.05 (607)	10
ANG	USA	b	-	0.26±0.02 (4722)	-	13
ANG	USA	b	-	0.25±0.02 (4722)	-	13
ANG	USA	b	0.19±0.002 *(9906)	-	-	11
ANG	USA	b	-	0.27±0.02 (2664)	-	12
ANG	USA	b	0.43±0.05	0.28±0.04	-	3
SIM	USA	d	-	-	0.21 (114899)	14
BSHH	Canada	b	-	-	0.25±0.05 (892)	4
LNR	UK	b	-	-	0.49±0.04 (896)	10
GHEF	USA	b	0.43 (603)	-	-	5
GHEF	USA	c	0.49 (603)	-	-	5
GHEF	USA	b	0.51 *(317)	-	-	15
GHEF	USA	b	0.34 *(256)	-	-	15
HEF and ANG	USA	b	0.42±0.04 (2351)	-	-	9
HEF, LNR and AANG	UK	b	0.43±0.02 (2196)	-	-	10
HEF and ANG	USA	c	-	-	0.48 (4838)	16
c) Yearling weight						
ANG	USA	b	0.21±0.04	0.48±0.04	-	3

Breeds: HEF, Hereford; ANG, Angus; BSHH, Beef Shorthorn; GHEF, Grade Hereford; RANG, Red Angus; AANG, Aberdeen Angus; SIM, Simmental; LNR, Lincoln Red.

Methods: a, correlation between consecutive records of the same cow; b, intra-class correlation; c, regression of later/ subsequent records on earlier records of the same cow; d, REML.

References:1, Gregory et al.(1950); 2, Cantet et al.(1988); 3, Alenda and Martin(1987); 4, Fahmy and Lalande(1973); 5, Botkin and Whatley(1953); 6, Bourdon and Brinks(1982); 7, Koger and Knox(1947); 8, Koch(1951); 9, Minyard and Dinkel(1965); 10, Kilkenny(1968); 11, Sellers et al.(1970); 12, Boston et al.(1975); 13, Hohenboken and Brinks (1969); 14,Wright et al.(1987); 15, Rollins and Wagnon(1956); 16, Cunningham and Henderson(1965b).

Figures in parentheses indicate number of observations.

* Steers.

weaning weight are higher than average heritability estimates for weaning weight. This supports the idea that maternal effects are important in determining the weaning weights of calves. The repeatability estimates for weaning weight are higher than those of birth weight.

The only estimates of the repeatability of yearling weight from the available literature are 0.21 for males and 0.48 for females (Alenda and Martin,1987). The higher estimate of repeatability of yearling weight in females than males may be due to the level of feeding in the post weaning period. The male calves were fed ad libitum allowing full expression of individual genetic variability for growth, while females were restricted to a rate of gain of approximately 0.5 kg per day. Restricted feeding probably created a dependency of post weaning gain on preweaning maternal environment in the females .

Most repeatability estimates have been calculated using intra class correlation and the regression of subsequent records on earlier record. Regression repeatabilities are unbiased by any truncation selection that has occurred based on earlier records (Curnow, 1961), whereas, the intraclass correlation repeatability of cow productivity considers all records at once; each regression coefficient reflects only the relationship between a specific pair of records of the same cow. A basic assumption for the estimation of repeatability using the regression of later records on earlier calf records of the same cow is that phenotypic variances are homogeneous for both variables.

The degree of adjacency of calf records affects the repeatability estimates. Cunningham and Henderson (1965b) have demonstrated that repeatabilities based on adjacent records tend to be higher than those based on non-adjacent records. It has been shown that repeatability decreases as the degree of adjacency increases. The number of pairs of

records in the estimate also decrease, leading to greater variance of the estimator and it is questionable whether estimate from pairs of records with a degree of adjacency of 5 or above are of much use. This decreasing trend in repeatability estimates has been discussed by Boston et al.(1975).The several factors suggested as the possible causes are:(i) positively correlated temporary environmental effects among consecutive or closely adjacent records of the same cow (e.g. closely related sires, management and nutrition practices, weather conditions and effects due to undefinable age of the dam), (ii) slight changes in the nature of permanent environmental effects acting on the cow which could be due to varying rates of physiological ageing (including the time of maturity and of the onset of the decline in production associated with age), or to partial recovery over time from an adverse heifer environment, and (iii) progressive selection of the cows.

An estimate of repeatability, like h^2, is merely a description of a certain population under certain conditions of the environment. The applicability of the estimate is therefore limited to those situations where (i) cattle are reared under conditions similar to those for which estimate was obtained, and (ii) the data are adjusted for the same sources of variation. The repeatability estimates can not be compared in a straight forward manner because repeatability is due to at least two components and the relationship between them. The cow gives her offspring half of her genes. Thus one fourth of the genes for growth of the calf are, on the average, common to maternal half-sibs. The second component involves maternal environment created for the calves of the same cow. This involves the expression of genes for the maternal performance of the cow in the trait expressed by her calves and permanent environmental effects common to calves by the same cow. If a covariance exists between genes for growth

and maternal ability, it may be either positive or negative: a negative covariance can mask a positive variance, making comparisons of repeatabilities difficult (Sellers et al., 1970).

2.5 Phenotypic, Genetic and Environmental Correlations

The phenotypic, genetic and environmental correlations between various performance traits (TABLES 2.11, 2.12, 2.13 and 2.15) have been estimated from different populations and it is therefore not surprising that differences exist. As these correlations vary between populations, estimates calculated from one environment should be generalised with certain caution. Environmental correlations are included only if given in the papers cited but they may be calculated from heritabilities and genetic correlations following the procedures outlined by Falconer (1989).

2.5.1 Weight Traits: The phenotypic, genetic and environmental correlations between birth weight and weaning weight are given in TABLE 2.11. The phenotypic correlations between the two traits range from 0.11 to 0.94 in various breeds. The average phenotypic correlation is 0.30 in males, 0.39 in females and 0.65 in combined data sets (TABLE 2.14). The correlations are positive and moderate to high in magnitude in almost all studies reviewed. These phenotypic correlations between birth weight and weaning weight do not necessarily mean that selecting on one trait will lead to improvement in the other, because a phenotypic correlation is not always a reliable estimate of the genetic relationship existing between the traits; an environmental effect upon two traits could be so strong that a negative genetic correlation is masked.

Estimates of genetic correlation between birth weight and weaning weight range from 0.25±0.34 to 0.99 ±0.01 in males, from 0.25±0.26 to 0.69 in females and from –0.36±0.22 to 0.83±0.02 across sexes. The negative

TABLE 2.11 Phenotypic, genetic and environmental correlations between birth weight and weaning weight

Breed	Country	Estimate									Reference
		Male			Female			Combined			
		r_P	r_A	r_E	r_P	r_A	r_E	r_P	r_A	r_E	
HEF	USA	-	0.99 ±0.01 (414)	-	-	-	-	-	-	-	1
HEF	USA	-	-	-	0.31 (748)	0.69	0.19	-	-	-	2
HEF	USA	0.35 (1769)	0.41	-	0.43 (1693)	0.53	-	-	-	-	3
HEF	UK	-	-	-	-	-	-	0.23	0.18 ±0.08	-	4
HEF	USA	-	-	-	-	0.48 (377)	-	-	-	-	5
HEF	USA	0.30 (1379)	0.37 ±0.17	-	-	-	-	-	-	-	6
HEF	USA	-	0.56 ±0.12	0.23	-	0.57 ±0.13	0.28	-	-	-	7
ANG	USA	0.33 (1101)	0.44 ±0.20	-	0.46 (1012)	0.61 ±0.26	-	0.39 (2113)	0.53 ±0.14	-	6

ANG	USA	0.35 (717)	0.59	-	-	-	-	-	-	-	8
ANG	USA	0.34	0.57 ±0.10	-	0.40	0.36 ±0.10	-	-	-	-	9
RANG	USA	-	-	-	-	-	-	0.38 (41184)	0.56 ±0.02	0.25	10
SIM	USA	-	-	-	-	-	-	0.34 (5578)	0.33 ±0.11	-	11
SIM	USA	-	0.42 ±0.12	-	-	0.30 ±0.10	-	-	0.33 ±0.07 (17297)	-	12
CHA	UK	-	-	-	-	-	-	0.23	-0.36 ±0.22	-	4
CHA	France	0.11 (647)	0.25 ±0.34	-	-	-	-	-	-	-	13
CHA	Canada	-	-	-	-	-	-	0.34 (1419)	0.47	0.32	14
SGT	USA	0.31 (939)	0.43 ±0.21	-	0.27 (955)	0.33 ±0.22	-	0.29 (1894)	0.40 ±0.14	-	15
BSHH	Canada	-	-	-	-	-	-	0.29 (892)	0.77 ±0.11	-	16
SDV	Nigeria	-	-	-	-	-	-	0.94 (31488)	0.83 ±0.02	-	17

Zebu	Nigeria	-	-	-	-	-	-	0.92 (23708)	0.81 ±0.01	-	17
HEF, ANG & RANG	USA	0.38	0.63 ±0.08	0.08	0.41	0.60 ±0.09	0.20	-	-	-	18
HEF, ANG & RANG	USA	-	-	-	0.31 (779)	0.25 ±0.26	0.33	-	-	-	19
CHA, BA & LIM	France	0.18 (2673)	0.46 ±0.16	-	-	-	-	-	-	-	13
ZX	Australia	-	-	-	-	-	-	0.43 (1267)	0.57	-	20
SBP	Canada	-	-	-	0.46 (505)	0.43 ±0.28	-	-	-	-	21

Breeds: HEF, Hereford; ANG, Angus; RANG, RedAngus; SIM, Simmental; CHA, Charolais; SGT, Santa Gertrudis; BSHH, Beef Shorthorn; SDV, South Devon; LIM, Limousin; BA, Blond d' Aquitaine; ZX, Zebu cross; SBP, Synthetic beef cattle population with approximately 33% Charlolais,33% Angus and 20% Galloway breeding with small contributions from other beef breeds.

References:1,Lasley et al.(1961); 2, Swiger(1961); 3, Koch et al.(1973); 4, Pabst et al.(1977); 5, Koch(1978); 6, Nelson and Kress (1979); 7, Buchanan et al.(1982); 8, Knights et al.(1984); 9, Alenda and Martin (1987); 10, Winder et al.(1990); 11, Burfening et al.(1978a); 12, Burfening et al.(1978b); 13, Renand(1985); 14, Johnston et al.(1992a); 15, Aaron et

al.(1987) ; 16, Fahmy and Lalande(1973) ; 17, Iloeje (1986); 18, Bourdon and Brinks(1982); 19, Smith et al.(1989); 20, Mackinnon et al.(1991); 21, Arthur and Makarechian (1992).

Estimates: r_P, phenotypic correlation; r_A, genetic correlation; r_E, environmental correlation.

Figures in parenthesis indicate number of observations.

TABLE 2.12 Phenotypic, genetic and environmental correlations between birth weight and yearling weight

Breed	Country	Estimate									Reference
		Male			Female			Combined			
		r_P	r_A	r_E	r_P	r_A	r_E	r_P	r_A	r_E	
HEF	UK	-	-	-	-	-	-	0.25	0.26 ±0.09	-	1
HEF	USA	-	-	-	-	0.60 (377)	-	-	-	-	2
HEF	USA	-	0.63 ±0.13	0.28	-	0.58 ±0.12	0.34	-	-	-	3
ANG	USA	0.43 (717)	0.57	-	-	-	-	-	-	-	4
ANG	USA	0.37	0.75 ±0.11	-	0.35	0.45 ±0.09	-	-	-	-	5
RANG	USA	-	-	-	-	-	-	0.39 (41184)	0.57 ±0.02	0.25	6
CHA	France	0.18 (699)	0.27	-	-	-	-	-	-	-	7
CHA	Canada	-	-	-	-	-	-	0.37 (1418)	0.46	0.35	8

HEF, ANG & RANG	USA	0.41	0.69 ±0.08	-0.01	0.40	0.55 ±0.11	0.25	-	-	-	9
HEF, ANG & RANG	USA	-	-	-	0.35 (779)	0.41 ±0.19	0.33	-	-	-	10
ZX	Australia	-	-	-	-	-	-	0.35 (1267)	0.47	-	11
SBP	Canada	-	-	-	0.45 (505)	0.53 ±0.19	-	-	-	-	12

Breeds: HEF, Hereford; ANG, Angus; RANG, Red Angus; CHA, Charolais; ZX, Zebu cross;SBP, Synthetic beef cattle population with approximately 33% Charolais,33% Angus and 20% Galloway breeding with small contributions from other beef breeds.

References:1, Pabst et al.(1977); 2, Koch(1978); 3, Buchanan et al.(1982); 4, Knights et al.(1984); 5, Alenda and Martin (1987); 6,Winder et al.(1990); 7,Renand and Gillard(1982); 8, Johnston et al.(1992a); 9, Bourdon and Brinks(1982); 10, Smith et al. (1989); 11, Mackinnon et al.(1991); 12, Arthur and Makarechian(1992).

Estimates: r_P, phenotypic correlation; r_A, genetic correlation; r_E, environmental correlation.

Figures in parenthesis indicate number of observations.

TABLE 2.13 Phenotypic, genetic and environmental correlations between weaning weight and yearling weight

Breed	Country	Estimate									Reference
		Male			Female			Combined			
		r_P	r_A	r_E	r_P	r_A	r_E	r_P	r_A	r_E	
HEF	USA	*0.70 (499)	0.10	0.76	0.57 (420)	0.18	1.07	0.65 (919)	0.16	0.83	1
HEF	UK	-	-	-	-	-	-	0.61	0.58 ±0.06	-	2
HEF	USA	-	-	-	-	0.71 (377)	-	-	-	-	3
HEF	USA	-	0.61 ±0.11	0.71	-	0.74 ±0.11	0.73	-	-	-	4
ANG	USA	0.71 (717)	0.79	-	-	-	-	-	-	-	5
ANG	USA	0.77	0.89 ±0.05	-	0.71	0.76 ±0.07	-	-	-	-	6
AANG	UK	-	-	-	-	-	-	0.57	0.38 ±0.12	-	2
RANG	USA	-	-	-	-	-	-	0.63 (41184)	0.78 ±0.02	0.57	7

SIM	Canada	-	-	-	-	-	-	-	0.63 (27788)	-	8
SIM	UK	-	-	-	-	-	-	0.63 (4461)	0.92	0.48	9
CHA	Canada	-	-	-	-	-	-	0.69 (1418)	0.47	0.73	10
DEV	UK	-	-	-	-	-	-	0.66	0.68 ±0.09	-	2
SDV	Nigeria	-	-	-	-	-	-	0.83 (23708)	0.74 ±0.02	-	11
SSX	UK	-	-	-	-	-	-	0.57	0.37 ±0.15	-	2
Zebu	Nigeria	-	-	-	-	-	-	0.85 (31488)	0.74 ±0.02	-	11
HEF & AANG	Canada	-	-	-	-	-	-	0.73 (84021)	0.80	0.71	12
HEF, ANG & RANG	USA	0.76	0.89 ±0.03	0.51	0.76	0.90 ±0.03	0.46	-	-	-	13
HEF, ANG & RANG	USA	-	-	-	0.79 (779)	0.84 ±0.09	0.79	-	-	-	14

ZX	Australia	-	-	-	-	-	-	0.76 (1267)	0.84	-		15
SBP	Canada	-	-	-	0.66 (505)	0.36 ±0.31	-	-	-	-		16

Breeds: HEF, Hereford; ANG, Angus; AANG, Aberdeen Angus; RANG, Red Angus; SIM, Simmental; CHA, Charolais; DEV, Devon; SDV, South Devon; SSX, Sussex; ZX, Zebu cross; SBP, Synthetic beef cattle population with approximately 33% Charolais,33% Angus and 20% Galloway breeding with small contributions from other beef breeds.

References:1,Blackwell et al.(1962); 2, Pabst et al.(1977); 3, Koch(1978); 4, Buchanan et al.(1982); 5, Knights et al.(1984); 6, Alenda and Martin(1987); 7, Winder et al.(1990); 8, Schaeffer and Wilton(1981); 9, Perez-Camara(1990); 10, Johnston et al.(1992a); 11, Iloeje(1986); 12, Kennedy and Henderson(1975b) ; 13, Bourdon and Brinks(1982); 14, Smith et al. (1989); 15, Mackinnon et al.(1991); 16, Arthur and Makarechian(1992).

Estimates: r_P, phenotypic correlation; r_A, genetic correlation; r_E, environmental correlation.

Figures in parenthesis indicate number of observations.

* Steer.

TABLE 2.14 Average phenotypic (r_P), genetic (r_A) and environmental (r_E) correlations between various growth traits

Traits correlated	Type of correlation	Male		Female		Steer		Combined	
		Average	Range	Average	Range	Average	Range	Average	Range
Birth weight and Weaning weight	r_P	0.30 (9)	0.11 to 0.38	0.39 (8)	0.27 to 0.46	-	-	0.65 (9)	0.23 to 0.94
	r_A	0.47 (11)	0.25 to 0.99	0.41 (10)	0.25 to 0.69	-	-	0.63 (10)	-0.36 to 0.83
	r_E	0.16 (2)	0.08 to 0.23	0.22 (3)	0.19 to 0.33	-	-	0.25 (2)	0.25 to 0.34
Birth weight and Yearling weight	r_P	0.37 (4)	0.18 to 0.43	0.39 (4)	0.35 to 0.45	-	-	0.39 (3)	0.25 to 0.39
	r_A	0.64 (4)	0.27 to 0.75	0.51 (5)	0.41 to 0.60	-	-	0.56 (3)	0.26 to 0.57
	r_E	0.14 (2)	-0.01 to 0.28	0.27 (2)	0.25 to 0.34	-	-	0.25 (2)	0.25 to 0.35
Weaning weight and Yearling weight	r_P	0.76 (3)	0.70 to 0.77	0.73 (5)	0.57 to 0.79	0.70 (1)	-	0.74 (8)	0.57 to 0.85
	r_A	0.88 (3)	0.61 to 0.89	0.76 (6)	0.18 to 0.90	0.10 (1)	-	0.76 (9)	0.16 to 0.92
	r_E	0.61 (2)	0.51 to 0.71	0.59 (3)	0.46 to 1.07	0.76 (1)	-	0.66 (5)	0.48 to 0.83

(Figures in parentheses indicate number of studies)

TABLE 2.15 Phenotypic, genetic and environmental correlations between birth, weaning and yearling weights and ultra-sonic backfat depth and muscling score

Breed	Country	Estimate									Reference
		Male			Female			Combined			
		r_P	r_A	r_E	r_P	r_A	r_E	r_P	r_A	r_E	
a) weaning weight and backfat depth											
HEF	USA	0.26 (578)	-0.01 ±0.63	-	-	-	-	-	-	-	1
HEF	USA	0.19 (824)	0.13 ±0.53	-	-	-	-	-	-	-	2
GHEF	USA	-0.13 *(679)	-1.00	-	-	-	-	-	-	-	3
b) Yearling weight and backfat depth											
HEF	USA	0.28 (695)	0.29 ±0.51	-	-	-	-	-	-	-	4
HEF	USA	0.29 (578)	0.19 ±0.43	-	-	-	-	-	-	-	1
HEF, ANG & PHEF	Australia	-	-	-	-	-	-	-	0.10 (9232)	0.34	5
c) Birth weight and muscling score											
HEF	USA	-	-	-	-	0.16 (377)	-	-	-	-	6
HEF	USA	-	0.18 ±0.16	0.10	-	0.12 ±0.19	0.05	-	-	-	7
CHA	France	0.08 (699)	0.38 ±0.28	-	-	-	-	-	-	-	8

BA, CHA & LIM	France	0.00 (3098)	-0.03 ±0.16	-	-	-	-	-	-	-	8
d) weaning weight and muscling score											
HEF	USA	-0.02 *(499)	-0.48	0.09	-0.15 (420)	-0.68	0.10	-0.07 (919)	-0.56	0.10	9
HEF	USA	-	-	-	-	-0.07 (377)	-	-	-	-	6
HEF	USA	-	-0.24 ±0.20	0.35	-	0.21 ±0.22	0.36	-	-	-	7
GHEF	USA	0.21 *(341)	0.38	-	-	-	-	-	-	-	3
CHA	France	0.03 (699)	-0.04 ±0.36	-	-	-	-	-	-	-	8
BA, CHA & LIM	France	-0.01 (3098)	-0.10 ±0.15	-	-	-	-	-	-	-	8
e) Yearling weight and Muscling score											
HEF	USA	0.27 *(499)	-0.66	0.27	-0.12 (420)	-0.77	0.58	-0.01 (919)	-0.65	0.35	9
HEF	USA	-	-	-	-	-0.19 (377)	-	-	-	-	6
HEF	USA	-	-0.14 ±0.20	0.56	-	0.04 ±0.03	0.56	-	-	-	7
CHA	France	0.27 (699)	0.08	-	-	-	-	-	-	-	10
HEF, ANG & PHEF	Australia	-	-	-	-	-	-	-	0.11 (3870)	0.29	5
f) Fat depth and Muscling score											
GHEF	USA	-0.09 *(341)	-0.46	-	-	-	-	-	-	-	3

HEF, ANG & PHEF	Australia	-	-	-	-	-	-	-	0.08 (3870)	0.10	5

Breeds: HEF, Hereford; CHA, Charolais; BA, Blond 'd Aquitaine; LIM, Limousin; GHEF, Grade Hereford; PHEF, Polled Hereford; ANG, Angus.

References:1, Neely et al. (1982); 2, Lamb et al.(1990); 3, Dinkel and Busch (1973); 4, Mavrogenis et al.(1978); 5, Robinson et al. (1992); 6, Koch(1978); 7, Buchanan et al.(1982); 8, Renand (1985); 9, Blackwell et al.(1962); 10, Renand and Gaillard (1982).

Estimates: r_P, phenotypic correlation; r_A,genetic correlation; r_E,environmental correlation.

Figures in parenthesis indicate number of observations.

* Steer.

estimate of genetic correlation between birth weight and weaning weight was reported by Pabst et al.(1977) from an analysis of the data on Charolais cattle. The small number of observations limits the conclusions which can be drawn from these findings. There are no similar estimates known from the literature except those from Willis et al.(1972) who obtained positive correlations between birth weight and weight at 90 days of age with pure-bred cattle but negative estimates with crosses. Cattle that had been graded up were included in the Charolais data and this may account for similar results. Most of the genetic correlations between birth weight and weaning weight are high and positive. They seem to indicate that the two traits are under the influence of similar genes and genetic change in one trait is expected to accompany a change in the other. The environmental correlation between birth and weaning weights are low to moderate.

The phenotypic, genetic and environmental correlations between birth weight and yearling weight are given in TABLE 2.12. The average phenotypic correlations between birth weight and yearling weight are positive and almost of similar magnitude (high) in males, females and across sexes (TABLE 2.14).

The genetic correlations are also positive and high ranging from 0.27 to 0.75 in males, 0.41 to 0.60 in females and 0.26 to 0.57 in combined data sets. It may be concluded from these estimates that the same genes tend to influence the two traits and that selection for one will improve the other as a correlated response i.e. higher birth weights will generally be associated with higher yearling weights.

The estimates of phenotypic, genetic and environmental correlations between weaning weight and yearling weight are presented in TABLE 2.13. The phenotypic correlations between weaning weight and yearling weight vary from 0.57 to 0.85 in different breeds. Most estimates of phenotypic

correlations between these two traits are high and positive (averages are 0.76 for males, 0.73 for females and 0.74 for combined sexes).

There is a very wide range in the genetic correlations between weaning weight and yearling weight in different breeds (0.16 to 0.92), with most of the estimates clustered around 0.80. It appears from these positive and high estimates that the two traits are affected by the same genes and selection for one trait will improve the other. A high and positive genetic correlation seems desirable because selection based on increased weaning weight will automatically improve yearling weight and will thus result in rapid and economical beef cattle production.

Most of the estimates of genetic correlations among body weights at various ages are moderate to high because of the part-whole relationship between them.

2.5.2 Weight Traits, Backfat Depth and Muscling Score:

The phenotypic, genetic and environmental correlations between weight traits and backfat depth and muscling score are given in TABLE 2.15. The estimates of phenotypic correlation between weaning weight and backfat depth range between 0.19 and 0.26 in males while in steers this correlation was –0.13, as reported by Dinkel and Busch (1973) from the analysis of data on grade Hereford steers. The genetic correlation varied from –0.01 to 0.13 in males while the figure for steers was –1.0. The phenotypic and genetic correlations between yearling weight and backfat depth are positive and low to moderate.

The phenotypic and genetic correlations between birth weight and muscling score are generally very low. It seems that there are very few genes that affect both traits and that there will be little correlated change in one trait as a result of selection for the other trait. It may be concluded that a high birth weight may not be a good indicator of muscling at yearling age.

The environmental correlations between birth weight and muscling score are also very low.

The phenotypic correlations between weaning weight and muscling score are low. The genetic correlations between weaning weight and muscling score vary very widely from –0.04 to –0.24 in males, from –0.68 to 0.21 in females and from –0.48 to 0.38 in steers. Reported values are very variable and inconclusive. For example, a genetic correlation of 0.38 between weaning weight and muscling score is moderate and it may be said that higher weaning weights may be associated with higher muscling scores at yearling age, while the value of –0.68 seems to indicate the reverse. The subjective nature of muscling score may account for the inconsistent estimates.

Yearling weight has been found to have a moderate phenotypic correlation with muscling score in bulls and steers (0.27), while in females this correlation was low and negative (–0.12). The genetic correlation between yearling weight and muscling score varied from –0.14 to 0.08 in males, from –0.77 to 0.04 in females and from –0.65 to 0.11 across sexes. The environmental correlations between yearling weight and muscling score are positive and high. They indicate that the two traits are affected by almost similar types of environments. This may be expected because an animal that is provided with the environmental conditions to increase muscularity will also put on weight.

2.6 Conclusions

The estimates of heritability for weight traits in beef cattle are generally moderate (0.25-0.30). They should, therefore, respond to selection. The estimates of direct heritability are higher than maternal heritabilities for all weight traits. Estimates of maternal heritability are highest for weaning weight, followed by yearling and birth weights in turn.

This indicates that maternal effects may be more important for weaning weight than for birth or yearling weight. This is further supported by the fact that the average repeatability estimate for weaning weight (trait of the dam) is higher than the average heritability for the trait (trait of the calf). Estimates of direct heritability for weight traits are moderate, while corresponding maternal heritability estimates range between low and low side of moderate. The estimates of direct and total heritability are almost of the similar magnitude for the three weight traits. Any of these traits can be expected to respond to selection even though the correlation between direct additive genetic and maternal additive genetic effects (r_{AM}) is negative. However, the rate of response will not be as high as expected if r_{AM} is zero. This negative correlation suggests that many of the same genes which favour milking and mothering ability of the cow are partly detrimental for growth of the young calf.

Ultrasonic backfat depth and visual muscling score are moderate to highly heritable.

The repeatability estimates of birth weight are lower than those for weaning weight, while that of yearling weight is low to moderate. The moderate repeatability of weaning weight indicates that selection on the basis of first record may be effective in improving the overall performance of the herd in the next year. It can be concluded that cows tend to repeat their previous performance to a higher degree for weaning weight of their calves than for birth weight.

The average genetic correlations between weight traits were generally moderate to high (0.41-0.88) as expected because of the part-whole relationship between them. The positive and high genetic correlation between birth weight and body weights at later ages seems to be undesirable, because this will increase the incidence of dystocia.

Therefore, it may be imperative to monitor birth weights, when selecting for higher weaning and yearling weights.

Weight traits do not seem to be highly genetically correlated with visual muscling score and backfat depth. The genetic correlation between muscling score and backfat depth appears to be moderate and negative , it seems that higher muscling scores are generally associated with decreased backfat depth.

Very wide ranges in the estimates of genetic parameters may be attributed to the following factors: (i) the number of observations in the analysis (ii) the method of analyses and estimation, (iii) the adjustments for non-genetic factors made on each data set, (iv) the genetic constitution of the breeds involved in the studies in different populations, (v) the number of measurements/records (h^2 and repeatability estimates may be different for single and multiple records), and (vi) sampling variance. The genetic parameters for various performance traits may be biased for the following reasons: (i) smallness of the dataset involved in the analyses, (ii) lack of appropriate statistical control over the possible environmental factors, (iii) selection, (iv) inbreeding, (v) assortative mating, (vi) an inappropriate method of estimation, and (vii) maternal effects .

There is a clear need for more thorough studies with large data sets using more sophisticated techniques of data analysis such as multivariate restricted maximum likelihood, particularly for the computation of genetic parameter estimates due to maternal effects on post weaning performance traits (yearling weight, muscling score and ultrasonic backfat depth). Very few studies have been found in the literature regarding genetic and phenotypic relationships between growth traits and muscling score and ultrasonic backfat depth. This suggests another area of future research, that may be vital for efficient and economical beef production namely the nature

of relationship between weight traits and ultrasonic backfat depth. There is also a serious deficiency in the current state of knowledge regarding the nature of genetic relationships between various performance traits as maternal effects may be a source of bias. Further investigations involving phenotypic and genetic analysis of the correlations between various performance traits including maternal effects in the model for analysis may, therefore, be warranted.

CHAPTER 3

MATERIALS AND METHODS

3.1 Introduction

A primary objective of research in animal breeding has been the attempt to predict accurately the breeding values of animals using mixed model methodology. Efficient application of this technique for the estimation of genetic potential of the animals requires precise and unbiased estimates of the genetic, phenotypic and environmental parameters.

The previous chapter has reviewed the considerable research efforts that have been directed towards the estimation of phenotypic, genetic and environmental parameters for various performance traits of beef cattle in different parts of the world. The studies involving genetic parameter estimates from the British beef cattle population are limited and scarce. The estimates published by Mrode and Thompson(1990) are the most recent, but the size of the dataset and analytical models used were the limiting factors.

The present study was thus initiated to explore the amount of phenotypic, genetic and environmental (co)variation amongst various performance traits of Simmental cattle in UK herds with the objective of generating the estimates of parameters using individual animal model restricted maximum likelihood procedures. In this chapter we review the materials and methods used. In chapter 4 univariate estimates of genetic parameters are presented and discussed while multivariate estimates are dealt with in chapter 5.

3.2 Description of the data

Pedigree and performance records of British Simmental cattle collected through the recording scheme of the Meat and Livestock Commission (1969 to 1991) from 1142 herds were utilised for the present investigation. Up to five traits, birth weight (kg), 200-day weight (kg), 400-day weight (kg), backfat depth (mm, average of the ultrasonic backfat depth measurements at two positions, over the eye muscle at the 13^{th} rib and the third lumbar vertebrae, at about 400 days of age) and muscling score (visual appraisal of the animal 's conformation and muscling on a scale of 1 to 15 at about 400 days of age), were measured on individual animals. Not all traits were measured on all animals.

Detailed information about the data preparation and fixed effect analyses and models for various performance traits is published elsewhere (Wray and Thompson, 1991). After a thorough analysis of the alternatives, the various fixed effects suggested are presented in TABLE 3.1. The month of birth, sex, (1, male ; 2, female), embryo transplant effect (1, normal ; 2, embryo transplant calf), birth type (1, single ; 2, twin) and contemporary group excluding sex were the fixed effects used for birth weight. The same fixed effects were fitted for 200-day weight except that, in addition, the effect of foster dam (1, normally reared calf ; 2, calf reared by the foster dam) was included. For 400-day weight, only month of birth, birth type and contemporary group including sex were considered. Birth type and contemporary group including sex were the two fixed effects fitted for both backfat depth and muscling score. Age of dam at birth (days) was fitted as a covariate (linear and quadratic) for weight traits, while for backfat depth and muscling score, age at measurement (days) was included as a covariate (both linear and quadratic).

TABLE 3.1 Fixed effect models used for each performance trait

Fixed Effects	Traits				
	Birth weight	200-day Weight	400-day Weight	Backfat Depth	Muscling Score
Month of birth	*	*	*		
Sex	*	*			
Embryo transplant calf	*	*			
Foster dam		*			
Birth type	*	*	*	*	*
Contemporary group excluding sex	*	*			
Contemporary group including sex			*	*	*
Age of dam at birth (linear and quadratic covariate)	*	*	*		
Age at measurement (linear and quadratic covariate)				*	*

Prior to the receipt of the data, a number of edits were performed which included the removal of standard birth weights and calculation of weights adjusted to a given age.

It was suspected that some birth weights were not recorded but had a 'standard' breed or farm weight inserted. Standard breed weight for females and males were 34 kg and 36 kg, respectively for 1985 and 39 kg and 41 kg, respectively, from 1986 to 1989. In order to attempt to eliminate farm standard, a procedure proposed by Wray and Thompson(1991) was used during construction of the dataset by the Meat and Livestock Commission. Records were ordered according to the contemporary groups, reading one contemporary group at a time. If more than 80 percent of both male and female records for any contemporary group were identical then that contemporary group was eliminated. It is not clear how effective at removing farm standards this procedure was.

The records of weaning and yearling weights were adjusted to 200 and 400-day basis using a within animal linear regression for each animal (Wray and Thompson,1991). In order to qualify for a 200 or 400-day weight an animal had to have a weight recorded within certain age limits. The limits used for these weights were: 170 to 300 days for 200-day weight and 270 to 500 days for 400-day weight. For animals which qualified for an adjusted weight, the adjustment used all records from birth to 300 days of age for 200-day weight and from 270 to 500 days of age for 400-day weight. It was recommended by Wray and Thompson (1991) that an additional adjustment using a population quadratic term for age at measurement is not required for 200 and 400-day weights because the term was non-significant for 400-day weight and it had a high standard error for 200-day weight.

The contemporary groups were formed taking into account the natural calving patterns (Wray and Thompson, 1991). Traditionally a contemporary group is considered to be a group of animals born within a specific three month period in a given year, in a given herd. This strategy of grouping ignores the natural calving patterns within a herd. This traditional way of grouping means that an animal born, say, in the last week of March will not be compared with another animal born in the first few days of April in the same herd under the same managemental conditions. Wray and Thompson (1991) introduced a method to take account of this and have contemporary groups as large as possible without any significant loss in contemporaneity. In this new approach animals are first ordered according to their date of birth within a herd. Then a search is carried out for the largest time gap between births within the first 90 days. Animals born before this gap will constitute the first contemporary group. This procedure of searching for the largest age gap is started again from the first animal after the age gap until the next largest age gap within the next 90 days is found. This is continued throughout the herd and is repeated for each trait of interest. When the number of animals within a particular contemporary group is less than five, this contemporary group is combined with an adjacent contemporary group, provided the overall age difference of the new contemporary group is less than 180 days. There were instances, when animals within these contemporary groups were managed differently, for example, sexes might be kept in different fields. Wherever information about such differential management was available, the contemporary groups were divided accordingly, provided the size of each of the new contemporary group was not less than five.

The data were checked for connectedness of contemporary groups by Wray and Thompson (1991). A contemporary group was considered

connected to the main dataset if a sire with a recorded offspring present in the contemporary group was also represented in the main dataset. Using this criterion, more than 99 percent of the 200-day weight records were in contemporary groups connected to the main dataset. They also standardised the records for heterogeneity of variance amongst herds for all traits, except muscling score, using procedures suggested by Brotherstone and Hill (1986).

In addition to the basic edits of consistency checks for dates, animal identities, removal of standard birth weights (breed averages) and other minor checks done by Wray and Thompson(1991), the following edits were conducted on the dataset by eliminating:

i) Birth weight, 200-day weight, 400-day weight and backfat depth records outside ±4.00 phenotypic standard deviations from the mean values of the corresponding traits within each contemporary group,

ii) the records of calves born to dams less than 21 months of age,

iii) the records of calves having age of dam at birth greater than ±4.00 standard deviations from the overall mean value of age of dam for a particular trait,

iv) all contemporary groups of size one for birth weight, 200-day weight, 400-day weight and backfat depth.

The number of records removed as a result of these edits for each performance trait used in the univariate analyses are given in TABLE 3.2.

Initially univariate datasets were constructed in order to give univariate estimates of phenotypic, genetic and environmental parameters. The birth weight dataset was the largest, comprising 31213 records. In order to reduce the computational load, it was decided to divide it into two datasets by splitting at random according to the herds. The characteristics of the datasets for the various performance traits along with the phenotypic

TABLE 3.2 Number of records removed during edits[a] of the dataset for univariate analyses

Trait	Total number of records	Age of dam at birth	Age of dam at birth	Trait	Cgs[b] of size one	Total records removed	Percent of total
		< 21 months	>±4.00 σ	>± 4.00 σ			
Birth weight	31433	88	26	48	58	220	0.70
200-day weight	27904	66	23	28	117	234	0.84
400-day weight	15570	25	17	18	270	330	2.12
Backfat depth	2055	-	-	1	2	3	0.15
Muscling score	1287	-	-	-	-	-	-

[a] Number of records removed from the dataset due to various edits as explained in the text; [b] Cgs, contemporary groups

average values and standard deviations for performance traits and ages are presented in TABLE 3.3.

For the preparation of bivariate data files for birth weight with backfat depth and muscling score, only those herds with records for birth weight were retained which had at least one animal with backfat depth and muscling score recorded. For bivariate growth trait combinations, i.e. birth weight with 200-day weight, birth weight with 400-day weight and 200-day weight with 400-day weight, animals bearing the same herd codes for the two traits in question were retained and then those herds were deleted which had only one of the two traits recorded. The number of records lost as a result of the earlier mentioned edits for various pairs of performance traits used in bivariate analyses are summarised in TABLE 3.4. Characteristics of the data structure for various combinations of traits used in bivariate analyses are given in TABLE 3.5.

3.3 Statistical Analyses

3.3.1 Univariate analyses: The data were analysed by the restricted maximum likelihood (REML) technique as proposed by Patterson and Thompson (1971) fitting an individual animal model. The estimates of (co)variance components were obtained by using the derivative-free restricted maximum likelihood set of programmes written by Meyer (1989). This analytical package, usually called DFREML, allows the inclusion of maternal genetic and maternal permanent environmental effects into the model of analyses. The different (co)variance component models employed for each trait are presented in TABLE 3.6. The models were numbered 1 to 6 after Meyer(1992). Model 1 may be regarded as the simple animal model with the animal 's direct additive genetic effect and the residual effect being the only random effects. Model 2 included maternal permanent environmental effects in addition to the random effects of model 1. In this

TABLE 3.3 Characteristics of the data structure for various performance traits used in the univariate analyses.

Traits	BWT 1 (kg)	BWT 2 (kg)	2WT (kg)	4WT (kg)	Fd (mmx100)	Ms(points)
No. of records	15598	15615	27670	15240	2052	1287
No. of animals	24714	25133	35510	22901	4911	3546
No. of sires[a]	2016	1988	2248	1741	647	493
	1349	1259	1898	1364	391	196
No. of dams[b]	9368	9773	11116	8440	2341	1790
	6547	6801	9689	6957	1392	886
No. of Cgs	2700	2669	4483	3527	245	145
Trait mean[c]	39.98 (3.29)	40.72 (3.53)	285.16 (30.25)	516.82 (41.70)	312.29 (69.37)	9.67 (1.08)
AOD mean[c]	2000.6 (995.8)	1979.6 (973.2)	2029.9 (1012.3)	2039.5 (1006.9)	-	-
AAM mean[c]	-	-	-	-	395.4 (41.1)	403.4 (42.8)
Birth years of records	1971 to 1991	1971 to 1991	1971 to 1990	1969 to 1990	1974 to 1990	1984 to 1990

[a]first line,total number of sires in the pedigree; second line, number of sires which have offspring with records.
[b]first line,total number of dams in the pedigree; second line, number of dams which have offspring with records.
[c]figures in parentheses are standard deviations. BWT 1, birth weight dataset 1; BWT 2, birth weight dataset 2; 2WT,200-day weight; 4WT,400-day weight; Fd, backfat depth; Ms, muscling score; Cgs,contemporary groups; AOD, age of dam at birth of the calf (days) ; AAM, age at measurement (days).

TABLE 3.4 Number of records removed during edits[a] of the dataset for bivariate analyses

Trait combination	Total number of records	Age of dam at birth of the calf	Age of dam at birth of the calf	Trait 1	Trait 2	Cgs of size one	Total records removed	Percent of total
		<21 months	>±4.00 σ	>± 4.00 σ	>± 4.00 σ			
Bwt and 2wt	21719	53	19	22	17	255	366	1.69
Bwt and 4wt	16544	39	16	21	14	306	396	2.39
Bwt and Fd	14344	46	14	23	1	22	106	0.74
Bwt and Ms	8782	29	10	12	-	10	61	0.69
2wt and 4wt	25903	69	23	28	25	241	386	1.49
2wt and Fd	28286	68	24	27	1	114	234	0.83
2wt and Ms	28146	68	24	27	-	117	236	0.84
4wt and Fd	15850	25	17	23	1	270	336	2.12
4wt and Ms	15859	25	17	23	-	270	335	2.11
Fd and Ms	2209	-	-	1	-	2	3	0.14

[a]Number of records removed from the dataset due to various edits as explained in the text; Bwt ,Birth weight; 2wt , 200-day weight; 4wt, 400-day weight; Fd, backfat depth; Ms, muscling score; Cgs, contemporary groups

TABLE 3.5 Characteristics of the data structure for various pairs of performance traits used in the bivariate analyses

Pairs of traits	Bwt and 2wt	Bwt and 4wt	Bwt and Fd	Bwt and Ms	2wt and 4wt	2wt and Fd	2wt and Ms	4wt and Fd	4wt and Ms	Fd and Ms
Number of Animals	28812	23635	20919	13480	33053	35987	35957	23267	23402	5216
Number of records	21353	16148	14238	8721	25517	28052	27910	15514	15524	2206
1st trait	396	5207	12244	7434	11310	26002	26625	13466	14240	919
2nd trait	8131	4115	1052	297	501	385	242	280	289	154
Both	12826	6826	942	990	13706	1665	1043	1768	995	1133
No. of sires[a]	1926	1712	1469	994	2125	2256	2248	1745	1742	657
	1539	1287	1059	587	1800	1918	1898	1373	1365	397
No. of dams[b]	9450	8301	7188	4842	10436	11271	11323	8575	8658	2484
	7794	6618	5632	3388	9051	9894	9897	7113	7175	1520
No.ofCgs										
1st trait	2082	1901	1654	875	4075	4483	4483	3526	3526	245
2nd trait	3394	2620	244	145	3397	245	145	245	145	145
Birth years of records	1971 to 1990	1969 to 1990	1971 to 1991	1971 to 1991	1969 to 1990	1971 to 1990	1971 to 1990	1969 to 1990	1969 to 1990	1974 to 1990

[a] First line ,Total number of sires in the pedigree; second line, number of sires which have offsprings with records.

[b] First line ,Total number dams in the pedigree ; second line, number of dams which have offsprings with records.

Bwt,Birth weight; 2wt,200-day weight; 4wt,400-day weight, Fd, backfat depth; Ms, muscling score; Cgs, contemporary groups.

TABLE 3.6 Variance / covariance component models employed for univariate analyses

Model	Component				
	σ^2_A	σ^2_M	σ_{AM}	σ^2_C	σ^2_E
1	*				*
2	*			*	*
3	*	*			*
4	*	*	*		*
5	*	*		*	*
6	*	*	*	*	*

σ^2_A, direct additive genetic variance; σ^2_M, maternal additive genetic variance; σ_{AM}, direct-maternal genetic covariance; σ^2_C, maternal permanent environmental variance; σ^2_E, residual variance.

model, maternal permanent environmental effect was fitted as an additional random effect assumed uncorrelated with the other random effects in the model. Model 3 attributed all maternal effects to the genotype of the dam. This maternal genetic effect was fitted as a second random animal effect with the same covariance structure as the direct additive genetic effects. In this model maternal additive genetic effect was assumed independent of the other random terms in the model. Model 4 was the same as model 3 except that it allowed for a covariance between direct additive genetic effects and the maternal additive genetic effects. Both maternal additive genetic and maternal permanent environmental effects were fitted together in model 5 with the covariance term between direct additive genetic and maternal additive genetic effects equal to zero. Model 6 was an extension of model 5, allowing for a covariance between direct additive genetic and maternal additive genetic effects.

The full model used to analyse the records (for example, 200-day weight) was:

$$Y_{ijklmnop} = M_i + S_j + E_k + F_l + B_m + C_n + b_1(AOD_{ijklmnop} - \overline{AOD}) + b_2(AOD_{ijklmnop} - \overline{AOD})^2 + a_o + m_p + en_p + e_{ijklmnop} \quad [1]$$

where,

$Y_{ijklmnop}$ is the 200-day weight record of the o^{th} calf ($o=1,...27670$);

born in the i^{th} month (M_i, $i=1,...12$);

of the j^{th} sex (S_j, $j=1$, male; 2, female);

k^{th} embryo transplant group (E_k; $k=1$, normal; 2, embryo transplant);

from l^{th} foster dam group (F_l; $l=1$, normal; 2, foster dam);

of m^{th} birth type (B_m; $m=1$, single; 2, twin);

raised in n^{th} contemporary group (C_n; $n=1,...4483$);

with $AOD_{ijklmnop}$ days of age of dam at its birth;

b_1 and b_2 are the linear and quadratic regression coefficients of weight on age of dam at birth;

$\overline{AOD}$ is the mean age of dam at birth;

a_o is the direct additive genetic effect of the o^{th} calf;

m_p is the maternal additive genetic effect of the p^{th} dam ;

en_p is the maternal permanent environmental effect of the p^{th} dam;

$e_{ijklmnop}$ is the random residual error pertaining to $Y_{ijklmnop}$.

The model [1] is a maternal animal model (Henderson, 1988; Meyer,1992) and can be written in matrix notation as a mixed model:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z_A u_A} + \mathbf{Z_M u_M} + \mathbf{Z_C u_C} + \mathbf{e}$$

The expected value and the variance of **y** are :

$$E(\mathbf{y}) = \mathbf{Xb}$$

$$V(\mathbf{y}) = \mathbf{V} = \mathbf{Z_A A Z_A}'\sigma_A^2 + \mathbf{Z_M A Z_M}'\sigma_M^2 + (\mathbf{Z_A A Z_M}' + \mathbf{Z_M A Z_A}')\sigma_{AM} + \mathbf{Z_C I_C Z_C}'\sigma_C^2 + \mathbf{I_N}\,\sigma_E^2$$

In the above,

y is a vector of records of the calves (27670 x 1);

X is the incidence matrix relating fixed effects to **y** (27670 x 4505);

b is the vector of fixed effects including the covariables (4505 x 1);

$\mathbf{Z_A}$ is the incidence matrix relating direct additive genetic effects to **y** (27670 x 35510);

$\mathbf{u_A}$ is the vector of direct additive genetic effects (35510 x 1);

$\mathbf{Z_M}$ is the incidence matrix relating maternal additive genetic effects to **y** (27670 x 35510);

$\mathbf{u_M}$ is the vector of maternal additive genetic effects (35510 x 1);

$\mathbf{Z_C}$ is the incidence matrix relating maternal permanent environmental effects to **y** (27670 x 9689);

$\mathbf{u_C}$ is the vector of maternal permanent environmental effects of the dam (9689 x 1);

$\mathbf{e}$ is the vector of residual environmental effects (27670 x 1);

$\mathbf{A}$ is the numerator relationship matrix between the animals (35510 x 35510);

$\mathbf{I_C}$ is the identity matrix of order equal to the number of dams (9689 x 9689); and

$\mathbf{I_N}$ is the identity matrix of order equal to the number of records (27670 x27670).

The random effects were assumed normally distributed with mean zero and variances:

$V(\mathbf{u_A}) = \mathbf{A}\,\sigma^2_A$

$V(\mathbf{u_M}) = \mathbf{A}\,\sigma^2_M$

$V(\mathbf{u_C}) = \mathbf{I_C}\,\sigma^2_C$

$Cov(\mathbf{u_A},\mathbf{u_M}) = \mathbf{A}\,\sigma_{AM}$

$V(\mathbf{e}) = \mathbf{I_N}\,\sigma^2_E$

where,

σ^2_A is the direct additive genetic variance;

σ^2_M is the maternal additive genetic variance;

σ_{AM} is the covariance between direct additive genetic and maternal additive genetic effects;

σ^2_C is the maternal permanent environmental variance;

σ^2_E is the residual variance.

It was also assumed that Cov ($\mathbf{u_A}$,$\mathbf{u_C}$), Cov ($\mathbf{u_A}$,$\mathbf{e}$), Cov ($\mathbf{u_M}$,$\mathbf{u_C}$),and Cov ($\mathbf{u_M}$,$\mathbf{e}$) are all zero.

The mixed model equations (Henderson, 1973) were of the following form:

$$\begin{bmatrix} X'X & X'Z_A & X'Z_M & X'Z_C \\ Z'_AX & Z'_AZ_A+A^{-1}\lambda_A & Z'_AZ_M+A^{-1}\lambda_{AM} & Z'_AZ_C \\ Z'_MX & Z'_MZ_A+A^{-1}\lambda_{AM} & Z'_MZ_M+A^{-1}\lambda_M & Z'_MZ_C \\ Z'_CX & Z'_CZ_A & Z'_CZ_M & Z'_CZ_C+I_C\gamma_C \end{bmatrix} \begin{bmatrix} \hat{b} \\ \hat{u}_A \\ \hat{u}_M \\ \hat{u}_C \end{bmatrix} = \begin{bmatrix} X'y \\ Z'_Ay \\ Z'_My \\ Z'_Cy \end{bmatrix}$$

Where,

A^{-1} is the inverse of the numerator relationship matrix (Henderson, 1976) and

λ_A, λ_M and λ_{AM} , are given by

$$\begin{bmatrix} \lambda_A & \lambda_{AM} \\ \lambda_{AM} & \lambda_M \end{bmatrix} = \sigma_E^2 \begin{bmatrix} \sigma_A^2 & \sigma_{AM} \\ \sigma_{AM} & \sigma_M^2 \end{bmatrix}^{-1}$$

$\gamma_C = \sigma_E^2 / \sigma_C^2$

The genetic parameters estimated were the direct heritability ($h_A^2=\sigma_A^2/\sigma_P^2$), the maternal heritability ($h_M^2=\sigma_M^2/\sigma_P^2$), the covariance between direct additive genetic and maternal additive genetic effects as a proportion of the phenotypic variance ($c_{AM}=\sigma_{AM}/\sigma_P^2$) and the genetic correlation between direct additive genetic and maternal additive genetic effects ($r_{AM}=\sigma_{AM}/\sqrt{\sigma_A^2\,\sigma_M^2}$). Another genetic parameter, usually called the total heritability (h_T^2), was calculated after Willham (1972) by the following formula:

$h_T^2 = (\sigma_A^2 + 1.5\,\sigma_{AM} + 0.5\,\sigma_M^2) / \sigma_P^2$

The terms in the numerator represent the covariance of the calf's total additive genetic effects with its phenotypic record. So the heritability represents all heritable genetic effects and can be visualised as the regression of the animal 's total genotype on its phenotype:

where,

σ_P^2 is the estimate of the phenotypic variance and

$\sigma_P^2 = \sigma_A^2 + \sigma_M^2 + \sigma_{AM} + \sigma_C^2 + \sigma_E^2$

The common environmental parameter estimated (c^2) represented the proportion of phenotypic variance attributable to the maternal permanent environmental effects and was calculated as follows:

$c^2 = \sigma_C^2 / \sigma_P^2$

All of the available pedigree information was included in the analysis in an attempt to minimise the bias due to selection and non random matings. It is expected to improve the accuracy and precision of the estimates. The convergence criterion (variance of the function values, –2 log likelihood) for various genetic, phenotypic and environmental parameters was $1x10^{-9}$.

The Likelihood ratio test as described by Rao (1973) and Mood et al. (1974) was used to compare the significance of random effects assumed in different models. The ratio [2(log L_i – log L_j)] asymptotically follows a chi-square distribution with degrees of freedom equal to the difference in the number of parameters used in model i (i = model 6) and j (j = models 1 to 5) with L the maximum likelihood value for model. Standard errors of the univariate estimates of h_A^2 , h_M^2 , c_{AM} and c^2 for various performance traits were calculated using the second derivative of the log likelihood function (Smith and Graser, 1986). This was accomplished by considering one parameter at a time and fixing its value at and above and below the maximum likelihood estimate. Then the log likelihood function was evaluated for all these points. Other parameters were kept fixed at their maximum likelihood values. For example, the log likelihood was estimated for different points of h_A^2 (points at and on either side of the maximum likelihood value), keeping all other parameters, i.e. h_M^2 , c_{AM} and c^2 at their

univariate maximum likelihood value. A quadratic equation $Y = a + bX + cX^2$ was fitted to the log likelihood and then the standard error of h^2_A was estimated by the following formula: S.E. $= \sqrt{-1/(2c)}$

3.3.2 Multivariate Analyses

The performance traits were analysed statistically for the multivariate estimation of genetic parameters using individual animal model restricted maximum likelihood (Patterson and Thompson, 1971). The fixed effects fitted for various performance traits in the multivariate analysis were the same as considered in the univariate estimation of genetic parameters (TABLE 3.1).

The multivariate individual animal model restricted maximum likelihood is very expensive in terms of computer time and memory required. For example, for N number of traits, the calculation of multivariate likelihoods, in general, takes of the order of N^2 as much space and N^3 as much time as a univariate analysis (Thompson and Hill, 1990). Therefore the analyses were carried out considering only two traits at a time. As the datasets were quite large, analyses were time consuming and computationally very demanding (e.g. in a bivariate case, with two variance components, i.e. σ^2_A and σ^2_E per trait, a total of 6 (co) variance components were to be estimated), the inclusion of maternal effects was not feasible. So, only a simple animal model involving the animal's direct additive genetic effects as the only random effect in addition to the residual effect was used in the bivariate estimation of genetic parameters.

The statistical model for the bivariate analysis may be built up from the following simple linear model for the univariate analysis:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{e} \qquad [2]$$

where,

y is the vector of observations of the animals (number of records x 1);

X is the known design matrix relating fixed effects to y (number of records x total number of fixed effect levels);

b is the vector of unknown fixed effects including the covariables (total number of fixed effect levels x 1);

Z is the known design matrix relating direct additive genetic effects to y (total number of records x total number of animals);

u is the vector of unknown random direct additive genetic effects (total number of animals x 1);

e is the vector of random residual effects (total number of records x 1).

The random effects were assumed normally distributed with mean zero and (co) variances:

$$V(\mathbf{u}) = \mathbf{G} = \mathbf{A}\,\sigma_A^2 \qquad V(\mathbf{e}) = \mathbf{R} = \mathbf{I}\,\sigma_E^2 \qquad \text{and} \qquad Cov(\mathbf{u},\mathbf{e}) = 0$$

$$V(\mathbf{y}) = \mathbf{V} = \mathbf{Z}\,\mathbf{A}\,\mathbf{Z}'\,\sigma_A^2 + \mathbf{I}\,\sigma_E^2$$

$$= \mathbf{Z}\,\mathbf{G}\,\mathbf{Z}' + \mathbf{R}$$

where,

A is the numerator relationship matrix (total number of animals x total number of animals);

I is the identity matrix (total number of records x total number of records);

σ_A^2 is the estimate of the direct additive genetic variance;

σ_E^2 is the estimate of the residual variance.

The mixed model equations corresponding to [2] can then be written as :

$$\begin{bmatrix} \mathbf{X}'\mathbf{X} & \mathbf{X}'\mathbf{Z} \\ \mathbf{Z}'\mathbf{X} & \mathbf{Z}'\mathbf{Z}+\mathbf{A}^{-1}\lambda \end{bmatrix} \begin{bmatrix} \mathbf{b} \\ \mathbf{u} \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{y} \\ \mathbf{Z}'\mathbf{y} \end{bmatrix}$$

Where,

$\mathbf{A}^{-1}$ is the inverse of the numerator relationship matrix and

$\lambda = \sigma_E^2 / \sigma_A^2$

The model [2] given above may then be extended for the bivariate analyses with different fixed effect models for each trait and can be written as follows:

$$\begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1 & 0 \\ 0 & \mathbf{X}_2 \end{bmatrix} \begin{bmatrix} \mathbf{b}_1 \\ \mathbf{b}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_1 & 0 \\ 0 & \mathbf{Z}_2 \end{bmatrix} \begin{bmatrix} \mathbf{u}_1 \\ \mathbf{u}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{I}_1 & 0 \\ 0 & \mathbf{I}_2 \end{bmatrix} \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \end{bmatrix} \quad [3]$$

where,

$\mathbf{y}_1$ and $\mathbf{y}_2$ are the vectors of observations for traits 1 and 2, respectively;

$\mathbf{X}_1$ and $\mathbf{X}_2$ are the design matrices relating fixed effects (relevant to each trait) to $\mathbf{y}_1$ and $\mathbf{y}_2$, respectively;

$\mathbf{b}_1$ and $\mathbf{b}_2$ are the vectors of unknown fixed effects pertaining to trait 1 and trait 2, respectively;

$\mathbf{Z}_1$ and $\mathbf{Z}_2$ are the design matrices relating direct additive genetic effects to $\mathbf{y}_1$ and $\mathbf{y}_2$, respectively;

$\mathbf{u}_1$ and $\mathbf{u}_2$ are the vectors of unknown random additive genetic effects for trait 1 and trait 2, respectively;

$\mathbf{I}_1$ and $\mathbf{I}_2$ are identity matrices ;

$\mathbf{e}_1$ and $\mathbf{e}_2$ are the vectors of random residual effects for trait 1 and trait 2, respectively.

The (co)variance structure assumed is :

$$V(\mathbf{u}) = \mathbf{G} = \begin{bmatrix} \mathbf{A}\sigma_{A_1}^2 & \mathbf{A}\sigma_{A_1A_2} \\ \mathbf{A}\sigma_{A_1A_2} & \mathbf{A}\sigma_{A_2}^2 \end{bmatrix};$$

$$V(\mathbf{e}) = \mathbf{R} = \begin{bmatrix} \mathbf{I}_1\sigma_{e_1}^2 & \mathbf{E}\sigma_{e_1e_2} \\ \mathbf{E}\sigma_{e_1e_2} & \mathbf{I}_2\sigma_{e_1}^2 \end{bmatrix} \text{ and}$$

$\text{Cov}(\mathbf{u},\mathbf{e}') = 0$

$V(\mathbf{Y}) = \mathbf{ZGZ}' + \mathbf{R}$

Where,

$\sigma_{A_1A_2}$ is the direct additive genetic covariance between trait 1 and trait 2;

$\sigma_{e_1e_2}$ is the residual covariance between trait 1 and trait 2;

E is the design matrix relating trait 1 to trait 2.

The DFREML set of programmes (Meyer,1991) was modified by Drs. Thompson and Crump (Roslin Institute, Roslin) according to the methodology proposed by Thompson et al.(1995) to do the analyses. All of the available pedigree information was included to improve the precision of the estimates. The convergence criterion, i.e. the variance of the function values (–2 log likelihood) in the simplex, was set at $1x10^{-9}$.

The various parameters estimated from the bivariate analysis were:

1) Heritability estimate (h_i^2) = $\sigma_{A_i}^2 / \sigma_{P_i}^2$

2) Phenotypic correlation (r_P) = $Cov_{P_iP_j} / \sigma_{P_i} \sigma_{P_j}$

3) Genetic correlation (r_A) = $Cov_{A_iA_j} / \sigma_{A_i} \sigma_{A_j}$

4) Environmental correlation (r_E) = $Cov_{E_iE_j} / \sigma_{E_i} \sigma_{E_j}$

where,

h_i^2 is the heritability of the i^{th} trait;

$\sigma_{A_i}^2$ is the aditive genetic variance for the i^{th} trait;

$\sigma_{P_i}^2$ is the phenotypic variance for the i^{th} trait;

$\sigma_{E_i}^2$ is the residual variance for the i^{th} trait;

$Cov_{P_iP_j}$ is the phenotypic covariance for traits i and j;

$Cov_{A_iA_j}$ is the additive genetic covariance for traits i and j;

$Cov_{E_iE_j}$ is the residual covariance for traits i and j;

3.3.3 Reparameterization of bivariate models

To simplify the fitting of bivariate models, they may be reparameterized to give uncorrelated residuals. Original models were of the form:

$$\mathbf{y_1} = \mathbf{X_1 b_1} + \mathbf{Z_{11}\, u_1} + \mathbf{e_1}$$

$$\mathbf{y_2} = \mathbf{X_2 b_2} + \mathbf{Z_{21}\, u_2} + \mathbf{e_2}$$

with

var $(\mathbf{u_1})$ $= \mathbf{A}\sigma^2_{A_1}$,

var $(\mathbf{u_2})$ $= \mathbf{A}\sigma^2_{A_2}$ and

cov$(\mathbf{u_1},\mathbf{u_2})$ $= \mathbf{A}\sigma_{A_{12}}$

The vectors $\mathbf{e_1}$ and $\mathbf{e_2}$ represent residuals of the individual animals. If both traits are measured on animal i then :

var $(\mathbf{e_{1l}}) = \sigma^2_{e_1}$, var $(\mathbf{e_{2l}}) = \sigma^2_{e_2}$ and cov$(\mathbf{e_{1l}},\mathbf{e_{2l}}) = \sigma_{e_{12}}$

This model involves six (co)variance parameters.

The above models were reparameterized (Thompson et al., 1995) such that:

$$\mathbf{y_1} = \mathbf{X_1 b_1} + \mathbf{Z_{11}}\, \mathbf{u_1} + \sigma^{*}_{e_1}\, \mathbf{Z_{12}}\, \mathbf{u_c}^{*} + \mathbf{e_1}^{*}$$

$$\mathbf{y_2} = \mathbf{X_2 b_2} + \mathbf{Z_{21}}\, \mathbf{u_2} + \sigma^{*}_{e_2}\, \mathbf{Z_{22}}\, \mathbf{u_c}^{*} + \mathbf{e_2}^{*}$$

The term $\mathbf{u_c}^{*}$ is introduced to allow environmental covariances between individuals. If $\mathbf{u_c}^{*}$ has variance σ^2_C then

$$\sigma^2_{e_1} = \sigma^{*2}_{e_1}(1+\sigma^2_C)$$

$$\sigma^2_{e_2} = \sigma^{*2}_{e_2}(1+\sigma^2_C)$$

$$\sigma_{e_{12}} = \sigma^{*}_{e_1}\sigma^{*}_{e_2}\sigma^2_C$$

The DFREML programme maximizes the likelihood using a search procedure in four dimensions. These correspond to

$$h^{*2}_1 = \sigma^2_{A_1}/\sigma^{*2}_{P_1};$$

$$h^{*2}_2 = \sigma^2_{A_2}/\sigma^{*2}_{P_2};$$

$$r^{*}_A = \sigma_{A_{12}}/(\sigma^{*}_{P_1}\sigma^{*}_{P_2}) \quad \text{and}$$

$$c^{*} = \sigma^2_C(\sigma^{*}_{e_1}\sigma^{*}_{e_2}/\sigma^{*}_{P_1}\sigma^{*}_{P_2})$$

with

$$\sigma^{*2}_{P_1} = \sigma^2_{A_1} + \sigma^2_C + \sigma^{*2}_{e_1};$$

$$\sigma^{*2}_{P_2} = \sigma^2_{A_2} + \sigma^2_C + \sigma^{*2}_{e_2}$$

For given values of h_1^{*2}, h_2^{*2}, r_A^* and c^*, then $\sigma_{e_1}^*$ and $\sigma_{e_2}^*$ can be found from residual sums of squares and cross products (Thompson et al., 1995), and (co)variances on the original scale can be generated.

3.3.4 Analysis of 200-day weight and 400-day weight

The bivariate combination 200-day weight and 400-day weight represented the most difficult bivariate analysis in terms of computing time because of the size of the dataset (with 33053 animals, 25016 records for 200-day weight and 14207 for 400-day weight) and fixed effect structure (4095 and 3411, total fixed levels for 200-day weight and 400-day weight, respectively), giving rise to a total of 99135 mixed model equations. The time required for each likelihood evaluation was very high. Therefore, it was considered impractical to iterate the analysis to a solution i.e. to maximise the log likelihood value for all of the parameters. It was decided to define a grid of points with respect to genetic and environmental covariance components, assuming a quadratic surface through the likelihood values evaluated under the premise that the estimates of other components would remain unchanged at their maximum likelihood values (Crump, 1992). It was shown by Crump (1992) in his analyses of pig data that the variance components from the iterative bivariate analysis were between 97.3 % and 100.9 % of the univariate estimates, thus justifying in his case the argument of fixing variance components at their univariate estimates.

A grid of 9 points consisting of all possible combinations of 3 values for each genetic and residual correlation was obtained using formulae given in the previous section (section 3.3.3), keeping the variance components at their univariate estimates. Then the log likelihood values were obtained for each point. The optimum combination of genetic and environmental correlations (e.g. A) in terms of log likelihood values was

assessed. After this, new grid points with dimension of the grid set close to A were evaluated. This process was continued until the "best" maximum likelihood value was obtained.

3.4 Likelihood Calculations

Consider the following linear mixed model

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{e} \qquad [4]$$

with **y**, **b**, **u** and **e** denoting the vectors of observations, fixed effects, random effects and residuals, respectively and **X** and **Z** the incidence matrices pertaining to **b** and **u**. Without loss of generality **X** is taken to be a full rank matrix.

Let $V(\mathbf{u}) = \mathbf{G}$ and $V(\mathbf{e}) = \mathbf{R}$ and $Cov(\mathbf{u}, \mathbf{e}') = 0$

so that

$V(\mathbf{y}) = \mathbf{V} = \mathbf{ZGZ}' + \mathbf{R}$

The terms in the mixed model equations can be written in terms of a c x c matrix **M** pertaining to [4], given by:

$$\mathbf{M} = \begin{bmatrix} \mathbf{y}'\mathbf{R}^{-1}\mathbf{y} & \mathbf{y}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{y}'\mathbf{R}^{-1}\mathbf{Z} \\ \mathbf{X}'\mathbf{R}^{-1}\mathbf{y} & \mathbf{X}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{X}'\mathbf{R}^{-1}\mathbf{Z} \\ \mathbf{Z}'\mathbf{R}^{-1}\mathbf{y} & \mathbf{Z}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{Z}'\mathbf{R}^{-1}\mathbf{Z}+\mathbf{G}^{-1} \end{bmatrix} = \begin{bmatrix} \mathbf{y}'\mathbf{R}^{-1}\mathbf{y} & \mathbf{r}' \\ \mathbf{r} & \mathbf{C} \end{bmatrix}$$

where,

C is the coefficient matrix and **r** the vector of right hand sides in the mixed model equations.

The likelihood can be written as follows (Meyer, 1989; Meyer,1991 and Meyer, 1994) :

$$\log L = -\frac{1}{2}\left[\text{constant} + \log|\mathbf{V}| + \log\left|\mathbf{X}'\mathbf{V}^{-1}\mathbf{X}\right| + (\mathbf{y} - \mathbf{X}\hat{\mathbf{b}})'\mathbf{V}^{-1}(\mathbf{y} - \mathbf{X}\hat{\mathbf{b}})\right]$$

or

$$\log L = -\frac{1}{2}\left[\text{constant} + \log|\mathbf{R}| + \log|\mathbf{G}| + \log|\mathbf{C}| + \mathbf{y}'\mathbf{P}\mathbf{y}\right] \qquad [5]$$

with

$$\mathbf{P} = \mathbf{V}^{-1} - \mathbf{V}^{-1}\,\mathbf{X}\,(\mathbf{X}'\mathbf{V}^{-1}\mathbf{X})^{-1}\,\mathbf{X}'\mathbf{V}^{-1}$$

Calculations of $|\mathbf{R}|$ and $|\mathbf{G}|$ are relatively straightforward by taking account of the structure of **R** and **G**. For instance **R** is diagonal in all the cases considered in this thesis and **G** can be calculated using properties of the additive relationship matrix (Quaas, 1976).

Graser et al.(1987) showed how $\log|\mathbf{C}|$ and $\mathbf{y}'\mathbf{P}\mathbf{y}$ can be found recursively by Gaussian elimination. For instance, if $\mathbf{M}_n$ (i,j) is the ijth element of a n x n matrix $\mathbf{M}_n$, then eliminating the nth row of $\mathbf{M}_n$ gives a (n−1) x (n−1) matrix $\mathbf{M}_{n-1}$. The elements of $\mathbf{M}_{n-1}$ can be calculated using :

$$\mathbf{M}_{n-1}(i, j) = \mathbf{M}_n(i, j) - (\mathbf{M}_n(i, n) \times \mathbf{M}_n(j, n) / \mathbf{M}_n(n, n) \qquad [6]$$

This can be thought of as eliminating the nth element of $\mathbf{x}_n$ from the system of equations $\mathbf{M}_n\,\mathbf{x}_n = \mathbf{y}_n$.

If $\mathbf{M}_c = \mathbf{M}$ then elimination of the last c−1 rows gives $\mathbf{M}_1$.

Then $\mathbf{M}_1(1,1)$ is $\mathbf{y}'\mathbf{P}\mathbf{y}$, the residual sum of squares, and

$$\log|\mathbf{C}| = \sum_{i=2}^{c} \log\,(M_i\,(i, i))$$

The time involved in forming [5] depends on the calculations in [6]. If no account is taken of the structure of $\mathbf{M}_n$ then the time is proportional to $c^3/6$ because at the ith stage i(i+1)/2 operations are needed. If, however, at the ith stage only m elements of the ith row are non-zero, then only m(m+1)/2 operations are needed in this stage.

The analysis of the data for the estimation of phenotypic, genetic and environmental parameters using the derivative-free (DF) REML algorithm may be facilitated by the proper ordering of the effects, i.e. fixed effects and animal effects (Meyer, 1989; Boldman and Van Vleck, 1991). Meyer(1989)

pointed out that the ordering of the equations in the augmented coefficient matrix (mixed model matrix) is crucial for minimising the number of off-diagonal non-zero elements. Thus in order to minimise the number of non-zero off-diagonal elements ("fill in") of the mixed model matrix during Gaussian Elimination (absorption) and to reduce the computation by keeping the matrices sparse, i.e. to speed up the analyses, several alternative ordering options were investigated :

Option A : i) Reorder animals, males followed by females, and ii) reorder females and offsprings which did not become parents in dam families. In this case, the order of the mixed model equations will then be as follows:

Trait + covariate + fixed effects + sires + non sires (dams + non parents)

Option B : i) Reorder males according to the number of descendants and the fixed effect (one with the highest levels, contemporary groups in the present study) according to its size, i.e. according to the number of individuals, in such a way that the most widely used popular sires and largest contemporary groups (Cgs) should be at the top. ii) Then reposition blocks of contemporary groups among the sires. iii) After this reorder females and offsprings which did not become parents into dam families.

In this scheme the order of the mixed model equations will be as follows:

Trait + covariate + other fixed effects + largest Cgs + most popular sires ...+ smallest Cgs + youngest bulls + nonsires (dams + non parents).

Option C : Use a minimum – degree algorithm (George and Liu, 1981) having graphical procedures to reorder the matrices used. This option essentially had 2 stages: i) calculate how many non-zero elements there are for each row, ii) eliminate one of the rows that had the least number of connections to the other rows. The procedure i) and ii) was repeated until all the rows were eliminated.

Option D : a minimum – degree algorithm with multiple elimination (Liu, 1985). This algorithm eliminated several of the least connected rows at the same time.

TABLE 3.7 illustrates the size of the "fill in" and the Central Processing Unit (CPU) time (seconds) obtained for the various approaches employed to facilitate the analysis of the data of backfat depth and 400-day weight (2052 records of ultrasonic backfat depth on 4911 animals having 247 total levels of fixed effects with 5161 mixed model equations *and* 15240 records of 400-day weight on 22901 animals, 3541 total fixed levels, 26445 mixed model equations in simple animal model settings).

It is evident that for the analysis of the data of backfat depth technique A resulted in 2.6 times fewer non-zero off-diagonal elements in the augmented coefficient matrix than the standard technique (S) where no reordering was performed. The use of technique A took 8.4 times less CPU time as compared to technique S. The techniques B, C and D further improved the situation and created 3.6, 9.4 and 9.5 times fewer non-zero off-diagonal elements than the technique S with 15.4, 70.6 and 70.6 times less CPU time for each round of likelihood evaluation than the standard technique. It is worth mentioning that for techniques C and D the time required for one likelihood evaluation was the same but technique D was found to be faster than technique C, i.e. technique C took 91.5 percent more CPU time for reordering of the mixed model equations than technique D. These conclusions are in agreement with Liu(1985).

For 400-day weight technique S was not attempted because of its high computational needs. The use of technique B on the dataset of 400-day weight resulted in 7.6 times fewer non-zero off-diagonal elements than technique A with a corresponding substantial reduction in CPU time (9.8 times). As for backfat depth, techniques C and D took the same CPU time

TABLE 3.7 Techniques considered to facilitate rapid Gaussian elimination of the mixed model matrix in the estimation of phenotypic, genetic and environmental parameters

Type of technique	Backfat depth			400-day weight		
	"Fill in" [a]	CPU[b] time[c] (sec)		"Fill in"	CPU time (sec)	
		ordering	absorption		ordering	absorption
Standard **(S)**	421030	-	494	-	-	-
a) reorder males followed by females **b)** reorder females and non parents in dam families **(A)**[d]	160100	-	59	7684306	-	13490
a) reorder males according to the number of descendants and fixed effect (one with highest number of levels ,contemporary groups in the present study) according to the number of individuals **b)** reposition blocks of contemporary groups (Cgs) as follows: biggest Cgs+ widely used bulls+...+smallest Cgs+ young bulls **c)** reorder females and non parents in dam families **(B)**[d]	115575	-	32	1010390	-	1379
Graphical ordering 1 **(C)**[d]	44850	59	7	172188	4701	427
Graphical ordering 2 **(D)**[d]	44296	5	7	172547	336	427

[a]"Fill in" is the number of non-zero off-diagonal elements of the augmented coefficient matrix; [b]CPU, central processing unit; [c]CPU time refers to the computer Dec Alpha 3000 / 400 with 112 MB of main memory; [d]technique as referred to in the text

(427 seconds) for each likelihood evaluation for 400-day weight, a considerable saving over techniques A and B. It may be concluded that the use of technique D seems worthwhile for use in routine analysis of the data as compared to other techniques because it not only generated less number of off-diagonal elements but also consumed less CPU time both for reordering and the calculation of [5] i.e. each likelihood evaluation. The order of these techniques in terms of their superiority may then be D, C, B, A. All these methods were used in the subsequent data analyses as appropriate and as experience was gained.

Even with reordering, the effort for calculation of [6] was not feasible for some models. Thompson et al.(1994) in a study of calculating approximate prediction error variances found that
if $\mathbf{M}_n(i, n) \times \mathbf{M}_n(j, n) / \mathbf{M}_n(n, n)$ in [6] is small and less than a threshold T, then disregarding this calculation: a) had little effect on prediction error variances, and b) reduced the amount of computation dramatically.

Similar results were found in this study in that the log-likelihood could be accurately calculated with $T= 10^{-6}$ and that the computation was reduced by a factor of at least 10 over exact calculation.

CHAPTER 4

UNIVARIATE ESTIMATES OF GENETIC PARAMETERS FOR VARIOUS PERFORMANCE TRAITS

4.1 Introduction

This chapter presents results from univariate analyses of the data described in chapter 3. The univariate estimation of parameters was carried out by restricted maximum likelihood fitting an individual animal model. Maternal effects and direct-maternal additive genetic covariance were fitted or ignored, to give six different models for each trait (TABLE 3.6). The details concerning the full model used are given in Chapter 3.

The analysis of each trait included all of the available pedigree information to reduce the bias due to selection and non random matings, thus improving the precision of the resulting estimates. The likelihood ratio test was used to test the significance of difference for parameter estimates across models (section 3.2). The genetic covariances between relatives were estimated from the (co)variance estimates obtained under different models for various weight traits using the information given in TABLE 4.1.

The computing characteristics of the univariate REML analyses for the weight traits are given in TABLES 4.2 to 4.5. The univariate analyses were completed using the following three computers as appropriate according to their availability at different times of the study period: i) Sun SPARC center 2000 with 256 MB of main memory, a multi-user system with four 50 MHz and two 40 MHz super SPARC CPUs. ii) Dec Station 5000 / 240 (MIPS 3000) with 64 MB of main memory. and iii) Dec Alpha 3000 / 400 with 112 MB of main memory. The CPU times in TABLES 4.2 to 4.5 are not comparable across models because of the use of different ordering options

TABLE 4.1 Composition of common covariances between relatives in terms of causal components (After Thompson,1976)

Relationship	Causal components of variance and covariance				
	σ^2_A	σ_{AM}	σ^2_M	σ^2_C	σ^2_E
Individual	1.00	1.00	1.00	1.00	1.00
Paternal half sibs	0.25	0.00	0.00	0.00	0.00
Maternal half sibs	0.25	1.00	1.00	1.00	0.00
Dam - offspring	0.50	1.25	0.50	0.00	0.00
Sire - offspring	0.50	0.25	0.00	0.00	0.00

σ^2_A, direct additive genetic variance; σ^2_M, maternal additive genetic variance; σ_{AM}, covariance between direct additive genetic and maternal additive genetic effects; σ^2_C, maternal permanent environmental variance; σ^2_E, residual variance.

TABLE 4.2 Computing characteristics of univariate REML analysis[a] for birth weight 1

Models	Total number of effects	CPU Time / likelihood evaluation (secs)	Total number of likelihood evaluations	Number of simplices
1 (A)[b]	27435	1592	18	8
2 (A+C)	33982	1768	44	20
3 (A+M)	52149	2079	38	19
4 (A+M+Cov_{AM})	52149	2128	253	122
5 (A+C+M)	58696	2610	128	62
6 (A+C+M+Cov_{AM})	58696	3572	136	71

[a]Analysis for models 1 to 4 was carried out on a Dec Station 5000 / 240 (MIPS 3000) with 64 MB of main memory, while analysis for models 5 and 6 was done on Dec Alpha 3000 / 400 with 112 MB of main memory.

[b]A, direct additive genetic effects; C, maternal permanent environmental effects; M, maternal additive genetic effects; Cov_{AM}, covariance between direct additive genetic effects and maternal additive genetic effects.

TABLE 4.3 Computing characteristics of univariate REML analysis[a] for birth weight 2

Models	Total number of effects	CPU Time / likelihood evaluation (secs)	Total number of likelihood evaluations	Number of simplices
1 (A)	27823	1456	23	10
2 (A+C)	34624	1678	46	21
3 (A+M)	52956	2872	42	19
4 (A+M+Cov_{AM})	52956	2816	78	40
5 (A+M+C)	59757	2826	126	60
6 (A+M+C+Cov_{AM})	59757	3100	137	76

[a]Analysis was carried out on a Sun SPARC center 2000 with 256 MB of main memory, a multiuser system with four 50 MHz and two 40 MHz super SPARC CPUs.
See TABLE 4.2 for abbreviations.

TABLE 4.4 Computing characteristics of univariate REML analysis[a] for 200-day weight

Models	Total number of effects	CPU Time / likelihood evaluation (secs)	Total number of likelihood evaluations	Number of simplices
1 (A)	40016	3394	24	11
2 (A+C)	49705	3810	54	27
3 (A+M)	75526	8918	52	26
4 (A+M+Cov_{AM})	75526	8893	78	41
5 (A+C+M)	85215	8696	75	36
6 (A+C+M+Cov_{AM})	85215	20379	147	78

[a]Analysis was carried out on a Sun SPARC center 2000 with 256 MB of main memory, a multiuser system with four 50 MHz and two 40 MHz super SPARC CPUs.

See TABLE 4.2 for abbreviations

TABLE 4.5 Computing characteristics of univariate REML analysis[a] for 400-day weight

Models	Total number of effects	CPU Time / likelihood evaluation (secs)	Total number of likelihoods evaluations	Number of simplices
1 (A)	26445	3103	25	11
2 (A+C)	33402	2911	58	27
3 (A+M)	49346	6986	45	19
4 (A+C+M+Cov_{AM})	49346	6045	116	55
5 (A+C+M)	56303	4179	106	47
6 (A+C+M+Cov_{AM})	56303	4804	167	75

[a]Analysis was carried out on a Dec Station 5000 / 240 (MIPS 3000) with 64 MB of main memory.
See TABLE 4.2 for abbreviations.

(section 3.4), but are given to highlight the size of the problem tackled in the present investigation.

4.2 Results and Discussion

The analyses of the data of 31213 records spread over 1142 herds indicated that the average birth weight (± standard deviation) was 40.4±3.5 kg. The averages for 200-day weight, 400-day weight, backfat depth and muscling score were 285.2±30.3 kg, 516.8±41.7 kg, 312.3±69.4 (mm x 100) and 9.7±1.1 points, respectively (TABLE 3.3).

The restricted maximum likelihood procedure has the property that the larger the value of the likelihood function, the better the model fits the data. In general each time when a parameter is added to the model, the likelihood value increases. Thus the likelihood values generally show an increasing trend from model 1 (simple animal model) to the most complicated model (model 6). TABLE 4.6 displays the results of the univariate estimation of (co)variance components in terms of the log likelihood values. The value of the log likelihood of each model expressed as a deviation from the most comprehensive model (model 6) has been used for the comparison of the results across models. Higher values in TABLE 4.6 indicate superiority of model 6 over other models in explaining the variation in the data set.

The (co)variance component estimates along with the resulting phenotypic, genetic and environmental parameters for various performance traits as obtained in the present study are described and discussed in the following under separate headings. The results are discussed in relation to the estimates obtained from the literature (chapter 2). However, In some cases, results are compared with other studies not included in chapter 2. Preference is given to those obtained for combined sex datasets from animal model REML procedures.

TABLE 4.6 Differences between the log likelihood obtained under model 6 and the respective log likelihood under models 1 to 5 for various performance traits.

Traits	Log L(model 6)–Log L(model n)				
	Model 1	Model 2	Model 3	Model 4	Model 5
Birth weight 1	45.58	14.57	17.21	10.13	7.83
Birth weight 2	25.13	1.08	14.13	14.11	0.30
200-day weight	69.39	16.31	15.42	15.22	0.55
400-day weight	11.82	4.87	3.11	2.15	0.90
Backfat depth	1.11	1.11	0.83	0.32	0.55
Muscling score	0.53	0.53	0.53	0.53	0.00

5 % level of significance $\chi^2_1 / 2 = 1.9$ $\chi^2_2 / 2 = 3.0$ $\chi^2_3 / 2 = 3.9$

4.2.1 Birth weight

The variance and covariance components and phenotypic, genetic and environmental parameter estimates for birth weight 1 and birth weight 2 are presented in TABLES 4.7 and 4.8, respectively. For both datasets ignoring maternal effects altogether (model 1) gave considerably higher estimates of the direct additive genetic variance (σ^2_A) and direct heritability (h^2_A) than other models. Fitting a maternal permanent environmental effect (model 2) increased the values of the log likelihood substantially over those of model 1, thus suggesting a significant maternal environmental effect on birth weight 1 and birth weight 2. The amount of variation explained by maternal permanent environmental effects was 8 (birth weight 2) to 9 percent (birth weight 1) of the total phenotypic variation in birth weight, with a corresponding reduction in the estimates of σ^2_A and h^2_A. Including a maternal genetic effect (model 3) resulted in a lesser increase in log likelihood over model 1 than model 2, i.e. model 2 provided a much better fit to the data than model 3 for both birth weight datasets, even though model 2 explained the variation in birth weight 2 better than the same model in birth weight 1. The maternal heritabilities (h^2_M) as obtained from model 3 were 0.09 and 0.06, respectively for birth weight 1 and birth weight 2, with the corresponding direct heritability estimates of 0.16 and 0.26, respectively.

It is evident from the likelihood values (TABLE 4.6) that dataset for birth weight 1 was best described by a model including both maternal additive genetic and maternal permanent environmental effects while for the birth weight 2 dataset inclusion of the both types of maternal effects did not improve much the likelihood values. The estimates of maternal permanent environmental effects (c^2) were quite consistent in the two birth weight datasets amounting to 0.07±0.01 (Model 6).

TABLE 4.7 Estimates of (co) variance components (kg^2) and genetic parameters[a] for birth weight 1

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
σ^2_A	3.44	2.07	1.92	2.81	1.82	2.77
σ^2_M	-	-	1.02	2.04	0.45	1.17
σ_{AM}	-	-	-	–1.28	-	–1.11
σ^2_C	-	1.02	-	-	0.72	0.80
σ^2_E	8.68	8.74	9.02	8.52	8.84	8.32
σ^2_P	12.12	11.83	11.96	12.09	11.83	11.95
h^2_A	0.28	0.18	0.16	0.23	0.15	0.23±0.03
h^2_M	-	-	0.09	0.17	0.04	0.10±0.01
c_{AM}	-	-	-	–0.11	-	–0.09±0.01
r_{AM}	-	-	-	–0.54	-	–0.62
c^2	-	0.09	-	-	0.06	0.07±0.01
h^2_T	0.28	0.18	0.20	0.16	0.17	0.14

[a] σ^2_A, direct additive genetic variance; σ^2_M, maternal additive genetic variance; σ_{AM}, covariance between direct additive genetic and maternal additive genetic effects; σ^2_C, maternal permanent environmental variance; σ^2_E, residual variance; σ^2_P,phenotypic variance; h^2_A ,direct heritability; h^2_M, maternal heritability; c_{AM}, σ_{AM} / σ^2_P ; r_{AM}, correlation between direct additive genetic and maternal additive genetic effects; c^2, σ^2_C/σ^2_P ; h^2_T, total heritability

TABLE 4.8 Estimates of (co)variance components (kg^2) and genetic parameters[a] for birth weight 2

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
σ^2_A	4.74	3.29	3.36	3.29	3.16	3.45
σ^2_M	-	-	0.73	0.69	0.13	0.19
σ_{AM}	-	-	-	0.06	-	–0.19
σ^2_C	-	0.97	-	-	0.89	0.93
σ^2_E	8.26	8.40	8.70	8.73	8.47	8.32
σ^2_P	13.00	12.66	12.79	12.77	12.65	12.70
h^2_A	0.37	0.26	0.26	0.26	0.25	0.27±0.03
h^2_M	-	-	0.06	0.05	0.01	0.02±0.01
c_{AM}	-	-	-	0.01	-	–0.02±0.01
r_{AM}	-	-	-	0.04	-	–0.24
c^2	-	0.08	-	-	0.07	0.07±0.01
h^2_T	0.37	0.26	0.29	0.29	0.26	0.26

[a]See TABLE 4.7 for abbreviations

For the birth weight 2 dataset estimates of the genetic covariance between direct and maternal effects (σ_{AM}) were essentially zero and resulted in little change in likelihood values as compared to the models ignoring it. Allowing for this covariance term for birth weight 1 dataset yielded a negative estimate amounting to 0.09±0.01 of the phenotypic variance (model 6), with a corresponding estimate of the genetic correlation between direct additive genetic and maternal additive genetic effects (r_{AM}) of –0.62. This resulted in a marked increase in log likelihood values.

In order to combine the results from the two birth weight datasets pooled estimates from Model 6 were calculated giving equal weight to the two datasets because of the approximate equality of the standard errors and numbers. Model 6 estimates were used because of the significant non-zero covariance between direct additive genetic and maternal additive genetic effects in birth weight dataset 1. Likelihood values using these pooled estimates were calculated for the two datasets. The likelihood values for each dataset were not significantly different from the corresponding likelihood calculated from the maximum likelihood estimates. Thus the average parameters in the two birth weight datasets fitted as well as maximum likelihood estimates in the two datasets. This bestowed some confidence on the average parameters for their use in genetic evaluations. The estimates of the average genetic and environmental parameters for various models for birth weight are presented in TABLE 4.9.

The average estimate of h_A^2 from model 1, which ignored maternal effects was 1.3 times the estimate from the complete model (model 6). The maternal effects in the complete model accounted for 13 percent of the total variance for birth weight. Inclusion of a maternal permanent environmental effect and a maternal genetic effect in the model resulted in a reduction in

TABLE 4.9 Average estimates of (co)variance components (kg^2) and genetic parameters[a] for birth weight

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
σ^2_A	4.09	2.68	2.64	3.05	2.49	3.11
σ^2_M	-	-	0.88	1.37	0.29	0.68
σ_{AM}	-	-	-	–0.61	-	–0.65
σ^2_C	-	1.00	-	-	0.81	0.87
σ^2_E	8.47	8.57	8.86	8.63	8.66	8.32
σ^2_P	12.56	12.25	12.38	12.44	12.25	12.33
h^2_A	0.33	0.22	0.21	0.25	0.20	0.25±0.02
h^2_M	-	-	0.07	0.11	0.02	0.06±0.01
c_{AM}	-	-	-	–0.05	-	–0.05±0.01
r_{AM}	-	-	-	–0.30	-	–0.45
c^2	-	0.08	-	-	0.07	0.07±0.01
h^2_T	0.33	0.22	0.25	0.23	0.22	0.20

[a]See TABLE 4.7 for abbreviations

direct heritability by about 33 and 36 percent, respectively, while consideration of both in the same model (model 5) reduced h^2_A by 39 percent.

The average estimate of h^2_A from the most comprehensive model (model 6) was 0.25±0.02 (TABLE 4.9). This value is slightly less than the average (0.30) estimate from the available literature (TABLE 2.9). Similar estimates of h^2_A (0.25 to 0.28) were reported by Bertrand and Benyshek (1987), Trus and Wilton (1988) and Kriese et al.(1991) in different breeds of beef cattle. Several other authors, however, have reported higher estimates of h^2_A in different breeds of beef cattle, For example the estimates of h^2_A in Simmental cattle were from 0.33 to 0.44 as reported by Trus and Wilton (1988), Garrick et al.(1989) and Swalve (1992).

Burfening et al.(1981) and Quaas et al.(1985), however, obtained lower estimates of h^2_A from the analyses of the data of American Simmentals. The estimates of h^2_A as reported by these workers were 0.21 and 0.16, respectively. Quaas et al.(1985) analysed the birth weight records of Simmental calves using an approximate REML procedure and observed h^2_A of the order of 0.16, which is at the lower tail of the literature estimates.

The h^2_A estimates reported in the literature for Hereford cattle ranged between 0.18 (Cantet et al.,1988) and 0.58 (Johnson et al.,1992). Meyer(1992) using similar models of analyses reported higher estimates of h^2_A (0.41) in Hereford cattle. In Angus cattle the range of direct heritability estimates was from 0.14 to 0.42.

The average h^2_M estimate for birth weight was 0.06±0.01 (TABLE 4.9). The literature h^2_M estimates (TABLE 2.9) showed a very wide variation from 0.03 (Hetzel et al.,1990) to 0.82 (Nelsen et al.,1984). However, similar h^2_M estimates ranging from 0.05 to 0.08 have been reported by many workers (Quaas et al.,1985; Bertrand and Benyshek, 1987; Hetzel et al.,1990; Meyer,1992; Meyer et al.,1992a; Meyer et al.,1992b; Swalve,1992; Shi et

al.,1993 and Waldron et al.,1993) in different breeds of beef cattle. Quaas et al.(1985) reported h^2_M estimate of 0.06 from the analyses of the birth weight records of American Simmentals using an approximate REML procedure. Meyer (1992) reported maternal heritability estimates of 0.07 and 0.08 in Angus and Hereford, respectively using individual animal model restricted maximum likelihood technique.

Higher estimates of h^2_M for birth weight, ranging between 0.21 and 0.82, have been reported by Brown and Galvez(1969), Nelsen et al.(1984), Cantet et al.(1988), Kriese et al.(1991) and Johnson et al.(1992) in different breeds of beef cattle.

The average estimate of the ratio of maternal permanent environmental variance to the phenotypic variance (c^2) was found to be 0.07±0.01 (TABLE 4.9). This estimate of c^2 is higher than that observed as the average (0.03) from the literature (TABLE 2.9). The findings of the present study on c^2 estimates are in line with those of Hetzel et al.(1990), who estimated c^2 to be 0.07 for birth weight of Africander cattle. A similar c^2 value (0.07) was reported by Waldron et al. (1993) from the analysis of the 2338 birth weight records of Angus cattle using a restricted maximum likelihood procedure. The studies involving estimation of c^2 for birth weight records of Simmental cattle are scarce in the available literature (chapter 2). In general, c^2 varied very widely from –0.38 in Angus cattle (Johnson et al.,1992) to 0.18 in Hereford Shorthorn cross (Hetzel et al.,1990). Johnson et al.(1992) analysed birth weight records of 2514 Angus calves and obtained an estimate of c^2 that was negative and high (–0.38).

Slightly lower c^2 estimates (0.03 for Angus and 0.05 for Hereford) than the present study were presented by Meyer (1992) using the REML technique from the more comprehensive model (model 6).

The average estimate of the covariance between direct and maternal genetic effects as a proportion of the phenotypic variance (c_{AM}) was –0.05±0.01 (TABLE 4.9). This is in line with the average estimate (–0.06) based on the results of 16 studies (TABLE 2.9). Similar estimates of c_{AM} amounting to –0.07 and –0.05 were also reported by Brown and Galvez (1969) and Johnson et al.(1992) in Angus and Hereford cattle, respectively. The estimate of the correlation between direct additive genetic and maternal additive genetic effects (r_{AM}) for birth weight was found to be –0.45 (TABLE 4.4) and in accordance with the findings of Quaas et al.(1985) who observed r_{AM} to be –0.44 from the analysis of American Simmental birth weights using approximate REML technique while r_{AM} estimates reported by Burfening et al.(1981),Trus and Wilton(1988), Garrick et al.(1989) and Swalve (1993) were –0.24, –0.22, –0.38 and –0.04, respectively, in Simmental cattle in different parts of the world.

Several other workers (Brown and Galvez, 1969; Nelsen et al.,1984; Cantet et al.,1988 and Kriese et al., 1991) have claimed r_{AM} to be high and negative ranging between –1.05 and –0.51 while low and negative r_{AM} estimates (–0.16 to –0.04) have also been reported (TABLE 2.6). On the contrary Trus and Wilton (1988), Mackinnon et al.(1991), Meyer (1992) and Waldron et al.(1993) have found r_{AM} estimates to be positive (0.01 to 0.55).

As already pointed out, the estimate of h^2_A (0.25±0.02) was substantially greater than the corresponding h^2_M estimate (0.06±0.01). This is in line with the findings of many workers (Burfening et al.,1981; Quaas et al., 1985; Bertrand and Benyshek,1987; Trus and Wilton, 1988; Johnson et al.,1992; Meyer,1992 and Swalve,1993). The opposite result was less frequently observed (Brown and Galvez,1969; Nelsen et al.,1984; Cantet et al.,1988; Kriese et al.,1991).

It seems from the results of the present study that the basis for maternal effects on birth weight was both genetic and environmental, both being equally important, even though the estimates are not very high. The h^2_A is moderate indicating thereby that birth weight may be changed by selection if desired. The negative genetic covariance term between direct and maternal effects has reduced the magnitude of the total heritable effects (h^2_T) for birth weight from h^2_A of 0.25 to h^2_T of 0.20. In spite of this decline in h^2_T, it still appears to be of reasonable size, such that selection would be effective.

In the present study the covariance between direct additive genetic effects and maternal additive genetic effects was negative and the resulting genetic correlation between direct and maternal effects was –0.45, which is quite high. Brown and Galvez (1969) are among several authors who also obtained negative and high r_{AM} from the analysis of the data of Hereford cattle. They stated that such a relationship indicates an antagonism between the genes for pre-natal growth and the genes conditioning the intra-uterine environment for heavier weight at birth. Such an antagonism would be a balanced mechanism with the tendency to maintain birth weights in intermediate ranges. This type of genic interaction seems desirable to minimise the incidence of calving difficulties. Their explanation for such a high and negative estimate seems plausible.

The estimates of covariances between relatives for birth weight 1 are given in TABLE 4.10. It appears that the covariance between half-sibs (both paternal and maternal) contributed about 7 percent of the phenotypic variance for model 1 (intra-class correlation) while the respective value for dam-offspring and sire-offspring covariances (regression of offspring on parent) was 14 percent. For model 2, where a maternal permanent environmental effect was included in addition to direct additive genetic effect, contribution of paternal half-sib covariance decreased by about 43 percent

TABLE 4.10 Estimates of between relative covariances for birth weight 1 under the 6 models

Relationship	Model 1 (A)	Model 2 (A+C)	Model 3 (A+M)	Model 4 (A+M+Cov_{AM})	Model 5 (A+C+M)	Model 6 (A+C+M+Cov_{AM})
Individual	12.12	11.83	11.96	12.09	11.83	11.95
Paternal half sibs	0.86 (7)	0.52 (4)	0.48 (4)	0.70 (6)	0.46 (4)	0.69 (6)
Maternal half sibs	0.86 (7)	1.54 (13)	1.50 (13)	1.46 (12)	1.63 (14)	1.55 (13)
Dam - offspring	1.72 (14)	1.04 (9)	1.47 (12)	0.83 (7)	1.14 (10)	0.58 (5)
Sire - offspring	1.72 (14)	1.04 (9)	0.96 (8)	1.09 (9)	0.91 (8)	1.11 (9)

Figures in the parentheses are the estimates of the covariances as a percentage of the phenotypic variance.
See TABLE 4.2 for abbreviations.

and of dam-offspring and sire-offspring covariance by about 36 percent with about 86 percent increase in the intra-class correlation between maternal half-sibs as compared to model 1. When direct additive genetic and maternal additive genetic effects were fitted together (model 3), the values for paternal and maternal half-sibs remained the same as for model 2 but the value of dam-offspring relationship increased by about 33 percent from 9 percent (model 2) to 12 percent (model 3). There was a slight decrease in sire-offspring covariance as compared to model 2. When both types of maternal effects (genetic and environmental) were considered together along with the covariance between direct additive genetic and maternal additive genetic effects (model 6) , the intra-class correlation of paternal half-sibs appeared to decrease by about 14 percent from a value of 7 percent for simple animal model to 6 percent for model 6. The increase in intra-class correlation of maternal half-sibs was about the same for model 6 as for other models including maternal effects. There seems to be a marked decrease (64 percent) in the estimate of the regression of offspring on dam from a value of 14 percent (model 1) to 5 percent (model 6). The decrease in the estimate of regression of offspring on sire was, however, 36 percent from model 1 to model 6.

The estimates of between relative covariances for birth weight 2 are presented in TABLE 4.11. For simple animal model higher values of intra-class correlation between paternal half-sibs and maternal half-sibs were observed for birth weight 2 (9 percent) as compared to birth weight 1.(7 percent). The same trend was observed for the regression of offspring on parent. These values were 18 percent for birth weight 2 as against the value of 14 percent for birth weight 1. For a detailed animal model (model 6), the contribution of paternal half-sibs decreased by 22 percent as compared to a simple animal model. This decrease is higher than that observed for birth

TABLE 4.11 Estimates of between relative covariances for birth weight 2 under the 6 models

Relationship	Model 1 (A)	Model 2 (A+C)	Model 3 (A+M)	Model 4 (A+M+Cov_{AM})	Model 5 (A+C+M)	Model 6 (A+C+M+Cov_{AM})
Individual	13.00	12.66	12.79	12.77	12.65	12.70
Paternal half sibs	1.19 (9)	0.82 (7)	0.84 (7)	0.82 (6)	0.79 (6)	0.86 (7)
Maternal half sibs	1.19 (9)	1.79 (14)	1.57 (12)	1.57 (12)	1.81 (14)	1.79 (14)
Dam - offspring	2.38 (18)	1.65 (13)	2.05 (16)	2.07 (16)	1.65 (13)	1.58 (12)
Sire - offspring	2.38 (18)	1.65 (13)	1.68 (13)	1.66 (13)	1.58 (12)	1.68 (13)

Figures in the parentheses are the estimates of the covariances as a percentage of the phenotypic variance
See TABLE 4.2 for abbreviations.

weight 1 (14 percent). The increase in the value of intra-class correlation for maternal half-sibs for birth weight 2 (55 percent) was less pronounced as compared to birth weight 1 (86 percent) for model 6 while the decline in the estimates of regression of offspring on parent was also less as compared to birth weight 1.

The maternal half-sib correlation was biased downwards for the simple animal model while the bias in the dam-offspring and sire-offspring regression was upwards.

As described earlier, the models involving a covariance term between direct and maternal effects for birth weight 1 (models 4 and 6) resulted in a significant increase in the log likelihood whilst the opposite was true for birth weight 2. For models 4 and 6 the estimates of intra-class correlation between paternal and maternal half-sibs were nearly the same for the two birth weight datasets but values of the regression of offspring on dam and regression of offspring on sire were considerably higher for birth weight 2 than birth weight 1. This may suggest that the relationship between offspring and parent might be contributing to this non-significant covariance term. Moreover, the estimates of regression of offspring on dam and the regression of offspring on sire were similar for birth weight 2 (12 and 13 percent respectively) while for birth weight 1 the respective values were 5 and 9 percent, respectively.

4.2.2 200-day weight

The estimates of (co)variance components along with the corresponding genetic and environmental parameters for 200-day weight as obtained in the present study for various models of analysis are presented in TABLE 4.12. Simple animal model (model 1) with out considering any maternal effects gave higher estimates of h^2_A as compared to models accounting for maternal effects. Inclusion of maternal permanent

TABLE 4.12 Estimates of (co) variance components (kg^2) and genetic parameters[a] for 200-day weight

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
σ^2_A	348.93	254.41	225.55	237.14	224.33	241.13
σ^2_M	-	-	80.07	88.29	37.19	44.76
σ_{AM}	-	-	-	–12.18	-	–14.78
σ^2_C	-	68.79	-	-	47.66	48.78
σ^2_E	601.19	605.94	630.60	624.46	618.47	609.71
σ^2_P	950.12	929.14	936.22	937.71	927.65	929.60
h^2_A	0.37	0.27	0.24	0.25	0.24	0.26±0.02
h^2_M	-	-	0.09	0.09	0.04	0.05±0.01
c_{AM}	-	-	-	–0.01	-	–0.02±0.01
r_{AM}	-	-	-	–0.08	-	–0.14
c^2	-	0.07	-	-	0.05	0.05±0.01
h^2_T	0.37	0.27	0.28	0.28	0.26	0.26

[a]See TABLE 4.7 for abbreviations.

environmental effects into the model of analysis (model 2) improved the likelihood values (TABLE 4.6) significantly over model 1, accounting for 7 percent of the total phenotypic variation in 200-day weight. A similar and significant trend in the likelihood values was observed when maternal additive genetic effects were fitted along with the direct additive genetic effects (model 3) and they accounted for 9 percent of the total variation for 200-day weight. The direct heritability was reduced from 0.37 (model 1) to 0.24 (model 3), a marked decrease of the order of 35 percent. Taking both types of maternal effects (genetic and environmental) into account together (model 5) gave a significantly better fit to the data than either model 2 or model 3. From the knowledge of the likelihood values given in TABLE 4.6, it seems evident that the covariance component between direct additive genetic effects and maternal additive genetic effects is not statistically significantly different from zero because of the small and non significant change in the likelihood values by the inclusion of the covariance term (log likelihood difference between model 3 and model 4 = 0.20, log likelihood difference between model 5 and model 6 = 0.55). The estimate of genetic covariance between direct and maternal effects (σ_{AM}) was negative and very low for both models 4 and 6. There was a little change in the h^2_T between the corresponding models.

The h^2_A estimate for 200-day weight as obtained from the most comprehensive model in the present study was 0.26±0.02 (TABLE 4.12). This estimate is close to the average estimate (0.22) obtained from the literature (TABLE 2.9). Similar results for h^2_A (0.24 to 0.28) have been also reported by Skaar(1985), Bertrand and Benyshek (1987), Kriese et al.(1991), Eler et al.(1992), Johnson et al.(1992) and Shi et al.(1993) in different breeds of beef cattle. Higher estimates ranging from 0.32 to 0.66 for h^2_A have been reported by Cantet et al. (1988), Garrick et al.(1989), Winder et al.(1990),

Johnson et al.(1992), Meyer (1992), Robinson and Rourke (1992) and Swalve (1992).

On the contrary many other authors (Skaar,1985; Graser and Hammond,1985; Quaas et al.,1985; Wright et al.,1987; Mrode and Thompson,1990); Wright et al.,1991; Kriese et al., 1991; Johnston et al.,1992b and Meyer,1992) have presented lower estimates of h^2_A for 200-day weight.

The estimates of h^2_A in Simmental cattle varied from 0.10 (Graser and Hammond, 1985) to 0.36 (Garrick et al.,1989). Mrode and Thompson (1990) reported a lower estimate of h^2_A for 200-day weight as compared to the findings of the present study. They analysed the 200-day weight records of British Simmental cattle (a subset of the data used in the present study) by animal model REML procedure. The h^2_A estimate was reported to be 0.19 (model 3) as against the value of 0.24 from the present study using the similar model.

The heritability estimate for the maternal additive genetic effects (h^2_M) on 200-day weight was 0.05±0.01 (TABLE 4.12). The value of h^2_M in the presented study appears to be in the lower tail of the literature results (TABLE 2.9). This value is about 62 percent less than the average estimate of h^2_M noticed in chapter 2. The estimates of h^2_M for 200-day weight have also been reported to be low by several other workers (Quaas et al.,1985; Mrode and Thompson, 1990; Robinson and Rourke, 1992).

However, the estimates of h^2_M were reported to be very high in the studies undertaken by Cantet et al.(1988), Wright et al.(1991), Eler et al.(1992), Johnson et al.(1992), Johnston et al.(1992b) and Meyer(1992) who reported the h^2_M estimates for weaning weight as 0.27, 0.47, 0.28, 0.43, 0.30 and 0.36, respectively in different breeds of beef cattle.

The maternal permanent environmental effect as estimated by the c^2 term was 0.05±0.01 (TABLE 4.12). This value is about 29 percent less than the average estimate obtained from the findings of studies conducted elsewhere (TABLE 2.9). However, similar results have been reported by Bertrand and Benyshek (1987,0.04 and 0.06 in Brangus and Limousin, respectively), Wright et al.(1987,0.07 in Simmental), Hetzel et al.(1990,0.06 in Africander cross), Mrode and Thompson (1990,0.08 in Simmental), Johnston et al. (1992b, 0.03 in Hereford), Meyer (1992,0.04 in Angus). On the other hand, Hetzel et al.(1990) and Meyer (1992) have presented higher values for c^2 term in different breeds of beef cattle. Meyer(1992) analysed the data of 7003 Hereford cattle using REML procedure and from the most comprehensive model c^2 term was reported to be 0.23, which is considerably higher than the estimate of the present study (0.05) from similar analysis.

The estimate of the covariance between direct additive genetic and maternal additive genetic effects as a proportion of the phenotypic variance (c_{AM}) was found to be negative and very low (–0.02±0.01) with a resulting estimate of the genetic correlation between direct and maternal effects of –0.14 (TABLE 4.12). This value of c_{AM} is about 29 percent of the average estimate obtained in chapter 2 from the published results (TABLE 2.9), and is in line with the findings of Johnson et al.(1992) who also observed low value of c_{AM} (–0.04) in Hereford cattle while studies conducted by Bertrand and Benyshek 1987), Garrick et al.(1989), Johnston et al.(1992b) and Meyer (1992) gave higher estimates of c_{AM} (from –0.05 to –0.36) in different breeds of beef cattle. Estimate of c_{AM} was observed to be zero by Mackinnon et al. (1991) from a study of the data of Zebu cross calves.

Contrary to the findings of many of these authors Graser and Hammond (1985), Wright et al.(1987) and Meyer (1992) have presented low but positive estimates of c_{AM} in Simmental and Angus cattle.

The estimate of h^2_A (0.26±0.02) was higher than the estimate of h^2_M (0.05±0.01) for 200-day weight in the present study. This result is similar to other estimates (chapter 2) obtained for Simmental cattle (Quaas,1985; Wright et al.,1987; Garrick et al.,1989 and Swalve, 1992) in different parts of the world. The same trend was observed in studies involving Hereford (Cantet et al.,1988; Johnson et al.,1992 and Meyer,1992), Angus (Skaar, 1985; Johnson et al., 1992 and Meyer,1992), Santa Gertrudis (Kriese et al.,1991) and Brangus (Bertrand and Benyshek,1987 and Kriese et al.,1991) cattle.

The maternal effects (both genetic and environmental) contributed about 10 percent of the total variation in 200-day weight and the two types of maternal effects appeared to be of equal importance in affecting 200-day weight. Similar studies from the British beef cattle population are scanty in the available literature. However, the results of research for maternal effects on the 200-day weight / weaning weight conducted in other parts of the world gave higher values ranging between 16 and 47 percent (Wright et al.,1987; Hetzel et al.,1990; Johnston et al.,(1992b); Meyer,1992 and Swalve,1992).

The estimates of covariances between relatives for 200-day weight are given in TABLE 4.13. For the simple animal model the value of intra-class correlation was 9 percent for both paternal and maternal half-sibs and regression of offspring on dam and regression of offspring on sire were both 18 percent. The inclusion of maternal effects into the analytical models (models 2 to 6) resulted in about 56 to 67 percent increase in the contribution of maternal half-sibs i.e. from 9 percent for simple animal model to 15 percent for the most comprehensive model. The values of other types of relationships showed a declining trend. As for birth weight, the estimate of the correlation of maternal half-sibs was biased downwards for the model ignoring maternal effects while the paternal half-sib correlation was biased

TABLE 4.13 Estimates of between relative covariances for 200-day weight under the 6 models

Relationship	Model 1 (A)	Model 2 (A+C)	Model 3 (A+M)	Model 4 (A+M+Cov_{AM})	Model 5 (A+C+M)	Model 6 (A+C+M+Cov_{AM})
Individual	950.12	929.14	936.22	937.71	927.71	929.60
Paternal half sibs	87.23 (9)	63.60 (7)	56.39 (6)	59.29 (6)	56.08 (6)	60.28 (6)
Maternal half sibs	87.23 (9)	132.39 (14)	136.46 (15)	135.40 (14)	140.93 (15)	139.04 (15)
Dam - offspring	174.46 (18)	127.21 (14)	152.81 (16)	147.49 (16)	130.76 (14)	124.47 (13)
Sire - offspring	174.46 (18)	127.21 (14)	112.78 (12)	115.53 (12)	112.17 (12)	116.87 (13)

Figures in the parentheses are the estimates of the covariances as a percentage of the phenotypic variance.
See TABLE 4.2 for abbreviations.

slightly upwards. The estimates of the regression of offspring on dam and regression of offspring on sire were greatly biased upwards for this model.

The results of the present study concerning maternal effects on 200-day weight reveal that the estimate of h^2_A is of moderate value and maternal effects are of slight importance and account for 10 percent of the phenotypic variance for 200-day weight. The estimates of h^2_A and h^2_T are of the same magnitude.

4.2.3 400-day weight

Variance and covariance components along with the estimates of genetic and environmental parameters for 400-day weight are shown in TABLE 4.14. It is evident that model 1 including only direct additive genetic effects and ignoring all maternal effects gave higher estimates of σ^2_A and h^2_A. Fitting maternal permanent environmental effect into the model along with the direct additive genetic effect (model 2) reduced the h^2_A by 13 percent from 0.39 to 0.34 with maternal permanent environmental effect contributing 4 percent to the total variance for 400-day weight. Likelihood ratio test (TABLE 4.6) revealed that model 2 fitted significantly better than model 1 in explaining the variation for 400-day weight. Including maternal additive genetic effect instead of maternal permanent environmental effect (model 3) resulted in a bigger reduction (18 percent) in h^2_A estimate as compared to model 2. The change in the log likelihood value for model 3 was also higher (over model 1) than for model 2. Thus suggesting a better fit of model 3 to the data over model 2. Considering both types of maternal effects in the same model (model 5), however, provided a significant increase in log likelihood values (TABLE 4.6) as compared to either model 2 or model 3, thus providing evidence for the existence of both types of maternal effects on 400-day weight, even though the extent is not very high. Fitting the

TABLE 4.14 Estimates of (co) variance components (kg^2) and genetic parameters[a] for 400-day weight

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
σ^2_A	705.33	608.87	571.61	623.51	560.67	629.61
σ^2_M	-	-	77.07	106.30	50.59	77.84
σ_{AM}	-	-	-	–48.27	-	–59.69
σ^2_C	-	76.62	-	-	46.98	53.73
σ^2_E	1112.30	1111.74	1148.31	1121.93	1133.73	1098.11
σ^2_P	1817.63	1797.23	1796.99	1803.47	1791.97	1799.60
h^2_A	0.39	0.34	0.32	0.35	0.31	0.35±0.03
h^2_M	-	-	0.04	0.06	0.03	0.04±0.01
c_{AM}	-	-	-	–0.03	-	–0.03±0.01
r_{AM}	-	-	-	–0.19	-	–0.27
c^2	-	0.04	-	-	0.03	0.03±0.01
h^2_T	0.39	0.34	0.34	0.34	0.33	0.32

[a]See TABLE 4.7 for abbreviations.

covariance term between direct additive genetic and maternal additive genetic effects (σ_{AM}) did not result in a significant improvement in log likelihood values over models omitting it, hence suggesting that the σ_{AM} estimate is not significantly different from zero.

The h^2_A estimate of 0.35±0.03 for 400-day weight is nearly the same as the average (0.31) of the findings elsewhere (chapter 2). Meyer(1992) and Swalve(1992) reported yearling weight direct heritabilities of 0.33 (Angus) and 0.37 (Simmental), respectively while the estimates of h^2_A for 400-day weight observed by Waldron et al.(1993) were 0.28 and 0.30, respectively in Hereford and Angus cattle. Meyer et al.(1992), however, presented lower h^2_A estimates of 0.16 and 0.25 for yearling weight in Hereford and Zebu cross animals. An estimate of around 0.27 for h^2_A of 400-day weight was reported by Mrode and Thompson(1990) from the analysis (model 2 and 3) of the records of British Simmental population, which is lower than the corresponding estimate of the present study from similar models.

Maternal additive heritability (h^2_M) of 0.04±0.01 for 400-day weight was 36 percent of the average (0.11) of the published estimates (TABLE 2.9) and is in the lower tail of these results. It is similar to the findings of Meyer(1992) from the analysis of the data of Angus cattle using individual animal model REML technique (model 6). The value of h^2_M was reported to be 0.04. Almost same value of h^2_M (0.06) was reported by Waldron et al.(1993) in Angus cattle, while in Herefords the h^2_M was found to be very low (0.01).

In contrast to the findings of the present study Meyer (1992) gave higher estimates of h^2_M (0.11 and 0.14) in Hereford and Zebu crosses, respectively. Swalve(1992) also reported a higher estimate of h^2_M (0.11) for yearling weight of Australian Simmental population.

The estimate of maternal permanent environmental variance as a proportion of the total phenotypic variance (c^2) was found to be 0.03±0.01

(TABLE 4.14). This estimate is in very close agreement with the average (0.03) value of the literature survey (TABLE 2.9). This is in close agreement with the average of estimates from the available literature(0.03). Similar c^2 values were also observed by Meyer (1992) in Angus (0.03) and Zebu cross animals (0.03) using similar models of analyses as used in the present study. However, in Herefords the c^2 value was slightly higher (0.05 and 0.06, respectively) as shown by Meyer(1992) and Waldron et al.(1993). Lower c^2 estimates of 0.01 and 0.02 for 400-day weight were given by Swalve (1992) and Waldron et al.(1993) in Simmental and Angus cattle, respectively using individual animal model REML procedure.

The covariance between direct additive genetic and maternal additive genetic effects as a proportion of the phenotypic variance (c_{AM}) is estimated to be −0.03±0.01, with the resultant genetic correlation between direct and maternal effects of −0.27 (TABLE 4.14). The value of c_{AM} as obtained in the present study is similar to that obtained as the average estimate (−0.04) from the published results (TABLE 2.9). This value is in line with the findings of Swalve (1992) who observed c_{AM} to be −0.05 (r_{AM} = −0.22). Meyer (1992) presented higher estimates of c_{AM} (−0.06 and −0.07, respectively) in Hereford and Zebu crosses and the r_{AM} were observed to be −0.48 and −0.39, respectively. In contrast to all of these results c_{AM} was reported to be positive (0.05) in Angus cattle by Meyer (1992) with the corresponding r_{AM} of 0.49. Positive estimates of c_{AM} were also reported by Waldron et al.(1993) from the analysis of yearling weight records of Herefords and Angus cattle. The c_{AM} estimates were 0.06 (r_{AM} = 0.97) in Herefords and 0.01 (r_{AM} = 0.07) in Angus cattle.

The estimate of direct heritability (0.35±0.03) was substantially higher than the estimate of maternal heritability (0.04±0.01) for 400-day weight. Similar results were reported from the review of literature (chapter 2) in

Herefords, Angus and Zebu cross animals (Meyer,1992) and Simmental cattle (Swalve,1992). This suggests that direct additive genetic effects are more important in influencing 400-day weight than maternal effects. On the whole maternal effects contributed about 7 percent of the total variation in 400-day weight, with maternal genetic effects slightly more important than maternal permanent environmental effects. Meyer (1992) also observed total maternal effects to be contributing about 7 percent of the total variation in Angus yearling weights, while in Herefords and Zebu cross animals, the corresponding figures were 16 percent and 17 percent, respectively as reported by Meyer(1992). In Simmental cattle maternal effects for yearling weight were shown to be 12 percent of the total variation by Swalve (1992).

The estimates of between relative covariance for 400-day weight under the 6 models are shown in TABLE 4.15. The contribution of paternal half sibs remained almost the same for different models with mild fluctuations. Thus maternal effects did not appear to bias the paternal half-sib correlation estimates for 400-day weight. The value of the intra-class correlation between maternal half-sibs increased by about 30 percent from 0.10 (model 1) to 0.13 (model 6). So it was biased downwards for the simple animal model. The rates of decline in the estimates of regression of offspring on dam and regression of offspring on sire were 20 and 15 percent, respectively for model 1 to model 6. Therefore, exclusion of maternal effects from the analysis created a upward bias in the estimates of regression of offspring on dam and regression of offspring on sire.

The estimates of (co)variance components and the resulting genetic and environmental parameters for 400-day weight seems to suggest that 400-day weight is mostly influenced by the genotype of the calf. The influence of maternal effects on 400-day weight though statistically significant is not very high. The estimate of r_{AM} is moderate but the likelihood ratio

TABLE 4.15 Estimates of between relative covariances for 400-day weight under the 6 models

Relationship	Model 1 (A)	Model 2 (A+C)	Model 3 (A+M)	Model 4 (A+M+Cov_{AM})	Model 5 (A+C+M)	Model 6 (A+C+M+Cov_{AM})
Individual	1817.63	1797.23	1796.99	1803.47	1791.97	1799.60
Paternal half sibs	176.33 (10)	152.22 (8)	142.90 (8)	155.88 (9)	140.17 (8)	157.40 (9)
Maternal half sibs	176.33 (10)	228.84 (13)	219.97 (12)	213.91(12)	237.74 (13)	229.28 (13)
Dam - offspring	352.66 (20)	304.44 (17)	324.34 (18)	304.57 (17)	305.63 (17)	279.11 (16)
Sire - offspring	352.66 (20)	304.44 (17)	285.81 (16)	299.69 (17)	280.34 (16)	299.88 (17)

Figures in the parentheses are the estimates of the covariances as a percentage of the phenotypic variance.
See TABLE 4.2 for the abbreviations used.

test revealed that it is not very different from zero. Thus the direct additive genetic and maternal additive genetic effects appear to be independent.

4.2.4 Backfat depth

The results of the present study concerning estimates of (co)variance components and genetic, phenotypic and environmental parameters for backfat depth are summarised in TABLE 4.16. It can be seen from the differences of log likelihood values given in TABLE 4.6 that the estimates from simple animal model ignoring maternal effects altogether were not statistically significantly different from those under other models. Inclusion of maternal permanent environmental effects (model 2) did not result in a significant change in log likelihood values over model 1 and the estimate of c^2 effects was negative and very low (almost zero). Fitting maternal additive genetic effects resulted in about 6 percent decrease in h^2_A i.e. from a value of 0.32 (model 1) to 0.30 (model 3) with maternal additive genetic effects contributing 3 percent of the total variance for backfat depth. This also did not improve log likelihood values significantly. The same trend in log likelihood values was evident when both types of maternal effects considered together in the same model (model 5) and for the detailed model (model 6) where all random components were fitted simultaneously. The log likelihood values suggest that trait is simply under the influence of direct additive genetic effects.

Similar studies for comparison involving influence of maternal effects on backfat depth are lacking in the available literature (chapter 2). The only study found is that of Robinson et al.(1992) who analysed the data of 9232 Angus, Hereford and Polled Hereford cattle aged 300 to 600 days at the scanning. The maternal additive genetic effects were reported to be 6 percent and 5 percent for ultrasonic rump fat and rib fat thickness,

TABLE 4.16 Estimates of (co) variance components and genetic parameters[a] for backfat depth and muscling score

component / parameter	Backfat depth			Muscling score
	Model 1	Model 3	Model 4	Model 1
σ^2_A	1630.56	1636.53	1789.16	0.30
σ^2_M	-	130.40	304.13	-
σ_{AM}	-	-	–299.46	-
σ^2_E	3464.93	3426.94	3318.88	0.86
σ^2_P	5095.49	5095.88	5111.88	1.16
h^2_A	0.32	0.30	0.35	0.26
h^2_M	-	0.03	0.06	-
c_{AM}	-	-	–0.06	-
r_{AM}	-	-	–0.41	-
h^2_T	0.32	0.32	0.29	0.26

For backfat depth, models 2, 5 and 6 resulted in negative estimates of the σ^2_C while for muscling score models 2 to 6 produced negative estimates of σ^2_C, zero estimates of σ^2_M and r_{AM} values of unity in models 4 and 6.
Standard errors for the direct heritability estimates from model 1 were 0.06 for backfat depth and 0.09 for muscling score.
[a] see TABLE 4.7 for abbreviations used.

respectively, while maternal permanent environmental effects contributed 4 percent and 11 percent of the total variation for rump and rib fat thickness. They observed that ignoring maternal effects resulted in a 2 to 5 percent upward bias in the estimates of h^2_A. The pooled mean direct h^2_A estimates were reported to be 0.37 and 0.30 for rump and rib fat thickness, respectively.

The maternal effects were not well estimated, the size and structure of the dataset being the main limiting factors. Only about 28 percent of the dams have more than one offspring with record for backfat depth (Figure 4.1). The h^2_A estimate from the present study (model 1) was estimated to be moderate (0.32±0.06) thus implying that ultrasonic backfat depth may be modified by selection. This is in close agreement with the average value of heritability (0.33) obtained from the literature (TABLE 2.5).

4.2.5 Muscling Score

The genetic and environmental parameters due to maternal effects along with the corresponding (co)variance component estimates are given in TABLE 4.16. A comparison of the log likelihood values (TABLE 4.6) obtained for different models indicates lack of significance of the estimates of (co)variance components apart from the direct additive genetic component. Thus it seems logical to conclude that muscling score is affected mostly by the direct additive genetic effects and maternal effects has no role to play in influencing the trait. As a matter of fact, the size and structure of the dataset used would indicate caution in putting complete trust in the results regarding maternal effects on muscling score. The dataset is not only small but it also seems not well structured for the disentanglement of the direct and maternal effects. About 75 percent of the dams have single offspring

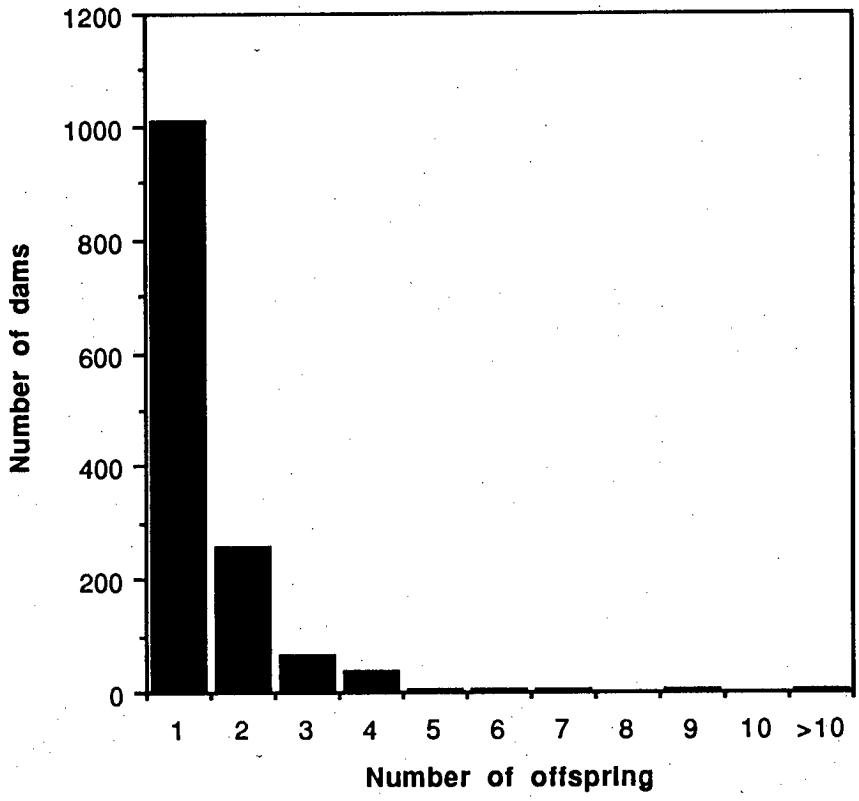

Figure 4.1: Number of offspring per dam for backfat depth

(Figure 4.2), thus they are not likely to contribute much information to the results.

The available published results regarding maternal effects on muscling score are scanty (chapter 2). The direct heritability estimate for muscling score as obtained in the present study was 0.26±0.09 (TABLE 4.16). This is close to the average (0.28) of the published estimates (TABLE 2.5). Robinson et al.(1992), however, presented lower estimates of heritability of 0.14 and 0.17 for muscling score from individual animal model REML analysis of the data of Herefords and Angus cattle, respectively. The pooled estimate of heritability was 0.15±0.07. The analysis of the Hereford and Angus cattle data by Francoise et al.(1973) using paternal half-sib correlation technique showed higher estimates of heritability than those of the present investigation.

Varying estimates of the heritability for muscling score may be partly explained by the subjective nature of the muscling score. Moderate estimate of heritability (0.26±0.09) for muscling score as obtained in the present study suggests that selection would be efficient for the improvement of this trait.

A wide variation in the genetic and environmental parameter estimates for various performance traits of beef cattle from the present study and those observed in the other investigations conducted worldwide may be attributed to methods of estimation, type of data set used i.e. experimental herds or field records, country of work, sex and breed of the animals, production and management systems, assortative mating and selection.

4.3 Conclusions

The analyses of the data of various performance traits of British Simmental cattle was performed using the restricted maximum likelihood technique. First of all a simple animal model, comprising the animal 's direct additive genetic effects was fitted. Subsequently various random effects

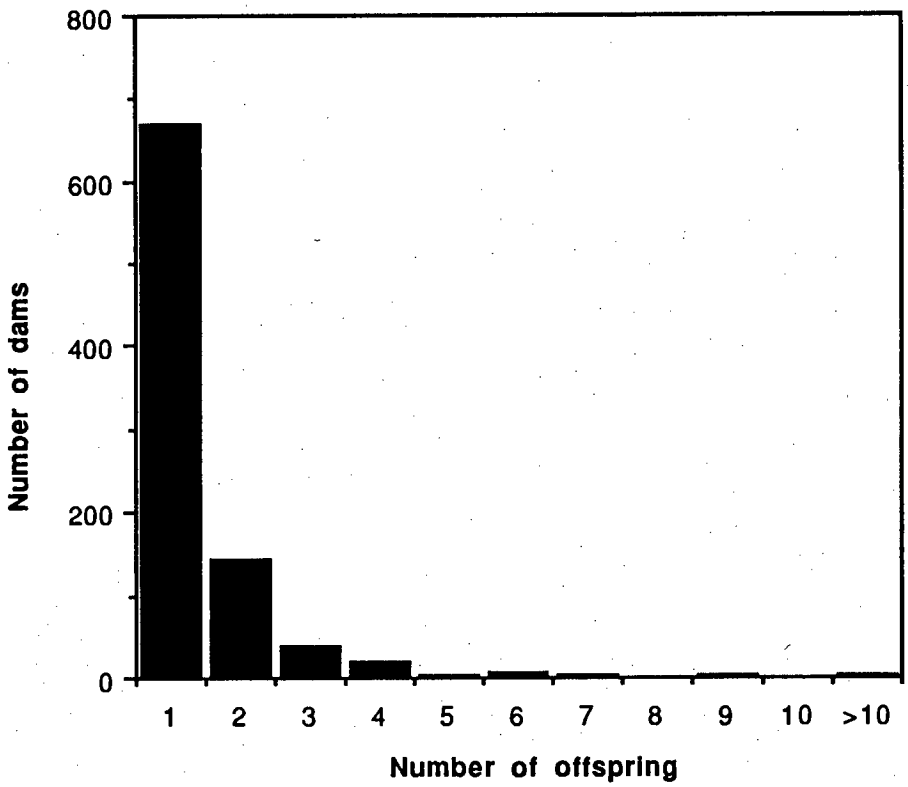

Figure 4.2: Number of offspring per dam for muscling score

(maternal additive genetic and maternal permanent environmental) were included in the model to ascertain their relative significance.

The estimates of genetic parameters due to maternal effects on various performance traits as observed in the 'best' model of the present study are shown in TABLE 4.17. It is interesting to note that the estimates of direct heritabilities for birth, 200-day and 400-day weights were higher than the corresponding estimates of maternal heritabilities for these traits. The sum of maternal additive genetic effects (h^2_M) and maternal permanent environmental effects (c^2) was also less than the corresponding direct additive genetic effects as measured by h^2_A. This implies that in the British Simmental population, weight traits are more affected by the calf 's own genes controlling the trait (direct effect) than those of the dam through her milking and mothering ability. This is in line with the findings of several other authors for these three weight traits (chapter 2).

It is argued from theory that maternal effects decline in importance with age viz. maternal effects tend to diminish in importance as the animal gets older. This is due to the fact that maternal effects become diluted with other environmental influences in later parts of the animal's life. This fact was supported by the findings of the present study as the maternal effects (h^2_M + c^2) contributed 13, 10, 7 percent of the total variation for birth weight, 200-day weight and 400-day weight, respectively.

Another notable and important feature is that maternal additive genetic and maternal permanent environmental effects were almost equally important for the three weight traits (birth weight, 200-day weight and 400-day weight). The results of the present study indicate that exclusion of maternal effects from the model of analysis for growth traits will somewhat overestimate the rate of genetic progress.

TABLE 4.17 Estimates of the genetic and environmental parameters[a] under the 'best[b]' model for various performance traits

Traits	h^2_A	h^2_M	c_{AM}	r_{AM}	c^2	h^2_T
Birth weight	0.25±0.02	0.06±0.01	–0.05±0.01	–0.45	0.07±0.01	0.20
200-day weight	0.26±0.02	0.05±0.01	–0.02±0.01	–0.14	0.05±0.01	0.26
400-day weight	0.35±0.03	0.04±0.01	–0.03±0.01	–0.27	0.03±0.01	0.32
Backfat depth	0.32±0.06	-	-	-		0.32
Muscling Score	0.26±0.09	-	-	-	-	0.26

[a]see TABLE 4.7 for abbreviations; [b] 'best' model meant the most comprehensive model (model 6) for birth weight, 200-day weight and 400-day weight, while for backfat depth and muscling score values are given for model 1 as the addition of different random components to model 1 did not result in significant improvement in the log likelihood for these two traits.

It is also of interest to note that the estimate of the covariance between direct additive genetic effects and maternal additive genetic effects as a proportion of the phenotypic variance was negative for the three weight traits studied. It was high (0.05) for birth weight, followed by 400-day weight (0.03) and 200-day weight (0.02). The resultant genetic correlations showed almost the same trend. The genetic correlation between direct additive genetic effects and maternal additive genetic effects for birth weight was found to be quite high (–0.45). It may be concluded from this negative and high estimate of the genetic correlation that the genes which control prenatal growth are partly incompatible with the genes which condition maternal (uterine) environment. This negative genetic correlation seems desirable to keep birth weights within limits, thus avoiding the huge economic losses due to dystocia and calving difficulties. Similar r_{AM} estimates have also been reported in other breeds from studies undertaken elsewhere (chapter 2).

A further feature of the present study is that the likelihood ratio test suggested the r_{AM} for 200-day weight and 400-day weight to be statistically not different from zero. So direct additive genetic and maternal additive genetic effects seem to be independent, i.e. selection for increased 200-day weight or 400-day weight (direct effect) will not result in a correlated response for milking and mothering ability. This may suggest that the genes which are responsible for the assimilation of nutrients for growth of the animal are independent of those genes which govern this process for lactation in the milking cow.

The existence of a true correlation between direct additive genetic and maternal additive genetic effects seems still inconclusive and a matter of some debate because even with the most sophisticated realistic models of analysis available today, it is usually assumed that the environmental covariance between dam and offspring is zero. This covariance term has

been advocated to be negative by several authors (for example, Koch,1972; Baker, 1980; Falconer,1989 and Garrick,1990). Such a negative environmental covariance between dam and offspring may result from the side effects of a high plane of nutrition of heifers during early periods of their growth on their milking and mothering ability, thus affecting weaning weights of their offspring. This means that the daughters of dams with good milking and mothering ability would provide inferior maternal environment for their offspring. Meyer (1992) points out that statistically this is equivalent to a negative covariance between the maternal environmental effects of dams and their daughters. Garrick(1990), while discussing this type of interaction between generations, suggests that a biological justification for this finding may be that excess adipose tissue is laid down in the mammary gland when a heifer calf grows too fast prior to weaning, impinging on its future lactational performance.

The inclusion of the covariance term between direct additive genetic and maternal additive genetic effects into the models (models 4 and 6) did not improve the log likelihood significantly over models ignoring it (models 3 and 5) for birth weight 2, 200-day weight and 400-day weight while for birth weight 1 a significant change was observed. A comparison of the estimates of covariances between relative for these traits (TABLES 4.10, 4.11, 4.13 and 4.15) interestingly revealed that for birth weight 1 the parent-offspring relationship contributed less (5 percent for dam-offspring and 9 percent for sire-offspring) than for other weight traits (12 percent dam-offspring ,13 percent for sire-offspring for birth weight 2; 13 percent both for dam-offspring and sire-offspring for 200-day weight and in case of 400-day weight the respective values were 16 and 17 percent, respectively). Moreover, for birth weight 1 the value of sire-offspring covariance was almost double that for dam-offspring covariance while for other weight traits both types of

covariances were almost equal in magnitude. This may be one of the reasons for significant negative covariance between direct additive genetic and maternal additive genetic effects observed in the present study for birth weight 1.

The estimates of the total additive heritable effects (h^2_T) for 200-day weight and 400-day weight are of almost the same magnitude as the estimates of the direct heritability (h^2_A).Thus the two traits may be expected to respond to selection. The h^2_T estimate for birth weight is slightly reduced due to the antagonistic relationship between direct additive genetic and maternal additive genetic effects.

The results of the present study concerning genetic parameters for the live animal traits, i.e. ultrasonic backfat depth and muscling score showed that the two traits were moderately heritable. This is in agreement with observations made from the review of the literature (chapter 2). Most of the observed variation for the two traits seemed to be under the influence of direct additive genetic effects. Maternal effects appeared to be of little importance for these two traits. Moderate estimates of heritabilities for backfat depth and muscling score indicate that direct selection would be effective in improving the two traits. The study revealed that different random effect models may be appropriate for different performance traits (Model 6 for birth weight, 200-day weight and 400-day weight and Model 1 for both backfat depth and muscling score).

Further investigations are needed with large and better quality data sets (if possible from embryo transfer and cross fostering trials) to effectively disentangle the direct and maternal effects, particularly for ultrasonic backfat depth and muscling score.

CHAPTER 5

MULTIVARIATE ESTIMATES OF GENETIC PARAMETERS FOR VARIOUS PERFORMANCE TRAITS

5.1 Introduction

Best linear unbiased prediction (BLUP) using the individual animal model (IAM) has become the worldwide standard for the prediction of breeding values of farm animals. Accurate estimates of genetic parameters are a prerequisite for the effective application of BLUP. It is generally considered desirable to estimate genetic parameters using restricted maximum likelihood (REML) with the same model as used to estimate breeding values.

In the univariate IAM REML analyses it is implicitly assumed that various performance traits are independent of each other, i.e. are uncorrelated (Meyer,1991). This is a very unrealistic assumption, since different traits may be correlated with one another as a result of pleiotropy, whereby a single gene affects two or more characters. The traits of body weights at different ages are correlated as a result of part-whole relationship as well. Moreover, in most animal breeding situations, data sets are not a random sample and they are generated either from planned selection experiments or field animal improvement programmes. There are arguments (e.g. Thompson, 1973) that suggest that REML estimates can provide unbiased estimates of genetic parameters in populations under selection and with culling of animals on the basis of early body weights. Thus multivariate IAM REML estimates are needed to: i) find out phenotypic and genetic relationships between various traits under consideration ii) predict the correlated responses to selection.

Therefore, the objectives of this study was to get more accurate and unbiased estimates of the genetic parameters for various performance traits

5.2 Materials and Methods

The records of British Simmental cattle on birth weight, 200-day weight, 400-day weight, backfat depth and muscling score collected from 1969 to 1991 were utilised for the multivariate estimation of genetic parameters. Unfortunately analyses of data considering all traits simultaneously was computationally not feasible. Thus bivariate analyses was carried out on all pairwise combinations of performance traits. Details of the characteristics of the data structure used in the present study for bivariate analyses have been given in chapter 3. The fixed effect models fitted were the same as were used for the univariate analyses (TABLE 3.1). An individual animal model restricted maximum likelihood procedure was followed for the statistical analyses. The DFREML set of programmes (Meyer,1991) modified by Drs. Thompson and Crump were used for the estimation of genetic parameters. As the datasets were quite large, analyses were computationally very demanding, so only the simple animal model attributing all of the genetic effects on performance traits to the genotype of the calf (direct effects) were fitted (see section 3.2.2 for details). All of the available pedigree information was included in the analyses. Likelihood ratios were used to test the null hypothesis that genetic correlations were zero (see section 3.3.1).

The computing characteristics of the bivariate REML analyses in terms of total number of effects, CPU time required for each likelihood evaluation, total number of likelihood evaluations and number of simplices required for each bivariate combination are presented in TABLE 5.1. The heritability estimates of weight gains and phenotypic, genetic and environmental correlations among them and between weight gains and

TABLE 5.1 Computing characteristics of bivariate REML analyses[a] for various performance traits

Trait combination	Total number of effects	CPU Time / likelihood evaluation (secs)	Total number of likelihood evaluations	Number of simplices
Birth weight and 200-day weight	84497	6555	254	140
Birth weight and 400-day weight	67977	3290	123	22
200-day weight and 400-day weight	99135	14997	22	-[b]
Birth weight and Backfat depth	58000	1834	155	86
200-day weight and Backfat depth	104782	5051	184	142
400-day weight and Backfat depth	65841	3458	150	77
Birth weight and Muscling score	36727	1309	131	74
200-day weight and Muscling score	104480	4362	282	199
400-day weight and Muscling score	66021	2061	273	151
Backfat depth and Muscling score	13038	353	81	43

[a]All analyses were carried out on Dec Alpha 3000 / 400 with 112 MB of main memory with the exception of the analysis of 400-day weight and backfat depth, which was carried out on Sun SPARC center 2000 with 256 MB of main memory, a multi user system with four 50 MHz and two 40 MHz super SPARC CPUs.

[b]This analysis was carried out by fixing the univariate estimates and by defining a grid of points with respect to genetic and environmental covariance components, assuming a quadratic surface through the likelihood values.

other performance traits were calculated from the estimates of (co) variances from the bivariate REML analyses. For example, the additive genetic variance for preweaning gain (gain from birth to 200 days) was calculated as follows:

$$V_{A_{(B\text{-}200)}} = V_{A_{(B)}} + V_{A_{(200)}} - 2\,Cov_{A_{(B,200)}}$$

where,

$V_{A_{(B\text{-}200)}}$ is the additive genetic variance for preweaning gain;

$V_{A_{(B)}}$ is the additive genetic variance for birth weight;

$V_{A_{(200)}}$ is the additive genetic variance for 200-day weight and

$Cov_{A_{(B,200)}}$ is the additive genetic covariance between birth weight and 200-day weight.

5.3 Results and Discussion

The estimates of phenotypic, genetic and environmental parameters (TABLES 5.2 to 5.5) obtained from the bivariate animal model REML analyses are discussed in the following, in relation to the literature estimates as given in chapter 2. Preference is given to those obtained for combined sex datasets from animal model REML procedures. The findings of the present study about the heritability estimates of weight gains and correlations among them and between weight gains and other performance traits (TABLES 5.6 to 5.9) are discussed in relation to some other work conducted elsewhere, not included in chapter 2.

5.3.1 Heritability estimates

The estimates of heritability for weight traits, backfat depth and muscling score from the bivariate REML analyses are presented in TABLE 5.2. These are generally consistent with the estimates from the simple animal model univariate analyses (chapter 4). The average (weighted by the number of observations for each trait in different bivariate combinations)

TABLE 5.2 Bivariate estimates of heritability and phenotypic variance for various performance traits

Trait combination	h_1^2	$\sigma_{P_1}^2$	h_2^2	$\sigma_{P_2}^2$
Birth weight and 200-day weight	0.34	12.77	0.36	943.32
Birth weight and 400-day weight	0.25	12.18	0.35	1749.62
200-day weight and 400-day weight[a]	0.37	945.74	0.39	2019.55
Birth weight and Backfat depth	0.36	12.17	0.29	5077.63
200-day weight and Backfat depth	0.37	949.03	0.31	5106.57
400-day weight and Backfat depth	0.39	1807.24	0.30	5071.54
Birth weight and muscling score	0.32	11.45	0.28	1.16
200-day weight and muscling score	0.37	948.48	0.28	1.19
400-day weight and muscling score	0.39	1803.93	0.22	1.13
Backfat depth and muscling score	0.32	5095.01	0.26	1.16

h_1^2, heritability estimate for the first trait; h_2^2, heritability estimate for the second trait; $\sigma_{P_1}^2$, phenotypic variance for the first trait; $\sigma_{P_2}^2$, phenotypic variance for the second trait; [a]heritability estimates from the univariate analysis; weight traits in kgs, backfat depth in (mm x100) and muscling score in points.

TABLE 5.3 Phenotypic covariance matrix (upper triangle) and phenotypic correlations (below diagonal) for various performance traits

Traits	Birth weight	200-day weight	400-day weight	Fat depth	Muscling score
Birth weight (kg)	-	30.74	27.34	12.43	0.36
200-day weight (kg)	0.28	-	1086.57	345.16	13.43
400-day weight (kg)	0.19	0.79	-	576.22	18.76
Backat depth (mmx100)	0.05	0.16	0.19	-	11.34
Muscling score (points)	0.10	0.40	0.42	0.15	-

TABLE 5.4 Additive genetic covariance matrix (upper triangle) and genetic correlations (below diagonal) for various performance traits

Traits	Birth weight	200-day weight	400-day weight	Backfat depth	Muscling score
Birth weight (kg)	0.32	23.22	17.57	7.36	0.43
200-day weight (kg)	** 0.60	0.37	503.97	166.64	4.65
400-day weight (kg)	** 0.41	** 0.96	0.38	149.81	5.69
Backfat depth (mmx100)	NS 0.09	* 0.22	NS 0.14	0.31	2.15
Muscling score (points)	** 0.39	** 0.43	** 0.44	NS 0.10	0.26

On the diagonal are the average (weighted by the number of observations for each trait in different bivariate combinations) estimates of heritability for various performance traits.

**, P<0.01 *, P<0.05 NS, P>0.05

TABLE 5.5 Environmental covariance matrix (upper triangle) and Environmental correlations (below diagonal) for various performance traits

Traits	Birth weight	200-day weight	400-day weight	Backfat depth	Muscling score
Birth weight (kg)	–	7.52	9.77	5.07	–0.07
200-day weight (kg)	0.11	–	582.60	178.52	8.78
400-day weight (kg)	0.10	0.68	–	426.41	13.06
Backfat depth (mmx100)	0.03	0.12	0.22	–	9.19
Muscling score (points)	–0.03	0.39	0.42	0.17	–

TABLE 5.6 Estimates of phenotypic variance of weight gains during various phases of growth (on the diagonal) and phenotypic correlations among weight gains and between weight gains and weight traits

Traits	Preweaning gain (kg)	Postnatal gain (kg)	Postweaning gain (kg)	Birth weight (kg)	200-day weight (kg)	400-day weight (kg)
Preweaning gain	894.61	0.84	0.17	0.17	0.99	0.82
Postnatal gain		1707.13	0.69	0.11	0.83	1.00
Postweaning gain			792.14	–0.04	0.16	0.74

Preweaning gain, gain from birth to 200 days; Postnatal gain, gain from birth to 400 days; Postweaning gain, gain from 200 to 400 days.

TABLE 5.7 Estimates of heritability of weight gains during various phases of growth (on the diagonal) and genetic correlations among weight gains and between weight gains and weight traits

Traits	Preweaning gain (kg)	Postnatal gain (kg)	Postweaning gain (kg)	Birth weight (kg)	200-day weight (kg)	400-day weight (kg)
Preweaning gain	0.33	1.00[a]	0.82	0.52	1.00	1.00[a]
Postnatal gain		0.34	0.73	0.35	1.00[a]	1.00
Postweaning gain			0.16	–0.25	0.72	0.89

Preweaning gain, gain from birth to 200 days; Postnatal gain, gain from birth to 400 days; Postweaning gain, gain from 200 to 400 days.

[a] Values truncated to unity as the estimates were greater than one.

TABLE 5.8 Estimates of environmental variance of weight gains during various phases of growth (on the diagonal) and environmental correlations among weight gains and between weight gains and weight traits

Traits	Preweaning gain (kg)	Postnatal gain (kg)	Postweaning gain (kg)	Birth weight (kg)	200-day weight (kg)	400-day weight (kg)
Preweaning gain	597.08	0.70	–0.03	–0.01	0.99	0.69
Postnatal gain		1130.40	0.70	0.01	0.70	1.00
Postweaning gain			662.54	0.03	–0.02	0.72

Preweaning gain, gain from birth to 200 days; Postnatal gain, gain from birth to 400 days; Postweaning gain, gain from 200 to 400 days.

TABLE 5.9 Estimates of phenotypic, genetic and environmental correlations between weight gains and backfat depth and muscling score

Trait combination	phenotypic correlation	genetic correlation	environmental correlation
Preweaning gain and backfat depth	0.16	0.23	0.12
Postnatal gain and backfat depth	0.19	0.15	0.21
Postweaning gain and backfat depth	0.12	–0.04	0.16
Preweaning gain and muscling score	0.41	0.44	0.39
Postnatal gain and muscling score	0.41	0.40	0.42
Postweaning gain and muscling score	0.18	0.17	0.18

Preweaning gain, gain from birth to 200 days; Postnatal gain, gain from birth to 400 days and Postweaning gain, gain from 200 to 400 days.

estimates of heritability were 0.32 for birth weight, 0.37 for 200-day weight, 0.38 for 400-day weight, 0.31 for ultrasonic backfat depth and 0.26 for the visual muscling score (TABLE 5.4). The estimates of heritability for weight gains during various phases of growth are given in TABLE 5.7. The heritability estimate for preweaning gain (gain from birth to 200 days) of 0.33 is higher than the estimates previously reported in the literature. For example, Davis(1993) presented a lower mean heritability estimate (0.16) for preweaning gain from a review of the published results in Northern Australia. Berruecos et al.(1978) and Burns (1991) also found lower values of heritability for preweaning gain in Brahman (0.22) and Africander cross (0.25) animals, respectively. Bourdon and Brinks (1982), however, reported higher estimates of heritability (0.60 in males and 0.66 in females) for preweaning gain in Red Angus, Angus and Hereford cattle as compared to the estimate of the present study.

The estimate of heritability for postnatal gain (gain from birth to 400 days) was 0.34 (TABLE 5.7). The moderate estimate of heritability for postnatal gain is higher than the estimate reported by Berruecos et al. (1978) in their study on Brahman cattle. Alenda and Martin(1987) in their work on Angus cattle, however, observed exactly similar estimate (0.34) of heritability for postnatal gain in males while in females the estimate reported was low (0.18).

The heritability estimate of postweaning gain (gain from 200 to 400 days) as observed in the present study was 0.16 (TABLE 5.7). This is lower than the average heritability estimate (0.31) for postweaning gain reported by Davis (1993) in his review. However, low estimates of heritability for postweaning gain have also been reported by Wilson et al.(1986). The performance records of 31443 Hereford and 24252 Angus cattle were analysed by paternal half-sib analysis. The heritability values for

postweaning gain reported from their study were 0.16 in Herefords and 0.15 in Angus. Perez-Camara(1990) observed a very low estimate of heritability for postweaning gain in Simmental cattle using a subset of the data used in the present study. The records of 4456 Simmental calves were analysed by individual animal model REML and the estimate of heritability was reported to be 0.09.

Contrary to the above findings, the estimates of heritability for postweaning gain as reported by Winder et al.(1990), Burns(1991) and Mackinnon et al.(1991) were higher and ranged from 0.26 to 0.43 in different breeds of cattle. Mackinnon et al.(1991) analysed the performance records of 1267 Zebu cross animals and the animal model REML estimate of postweaning gain was found to be 0.26. Bishop(1992) also found a higher estimate (0.37) of heritability for postweaning gain from the animal model REML analyses of the records of 542 Hereford bull calves.

The weight traits, preweaning gain, postnatal gain, backfat depth and muscling score, all appear to be moderately heritable. Interestingly for postweaning gain low additive genetic variation has been observed. The heritability estimate for postweaning gain may be biased downwards because of some culling based on 200-day weights but from the available data (field records), it is not very easy to exactly figure out the possible effects of selection.

5.3.2 Correlations between traits

Relationships between various performance traits expressed in terms of phenotypic, genetic and environmental correlations are shown in TABLES 5.3 to 5.9. The terminology adopted for the discussion of the magnitude of the various types of correlations (absolute value) is as follows: 0.00-0.25, low; 0.26-0.50, moderate; 0.51-0.75, high and 0.76-1.00, very high.

5.3.2.1 Correlations among weight traits

The estimate of the *phenotypic correlation* between **birth weight and 200-day weight** was 0.28 (TABLE 5.3). This is lower than the average estimate of phenotypic correlation (0.65) from the available literature, probably in the lower tail of the literature estimates (TABLE 2.14). Similar estimates of phenotypic correlation between birth weight and weaning weight (0.29) have been reported by Fahmy and Lalande (1973) in Beef Shorthorn and by Aaron et al.(1987) in Santa Gertrudis cattle. The estimate of phenotypic correlation between birth weight and 200-day weight as reported by Pabst et al.(1977) was 0.23 in Hereford and Charolais cattle. Burfening et al. (1978a), Nelsen and Kress (1979) and Winder et al.(1990), however, reported higher estimates (0.34 to 0.39) of phenotypic correlation between birth weight and weaning weight in Simmental, Angus and Red Angus cattle, respectively. Very high estimates of phenotypic correlation between birth weight and weaning weight as compared to the present study have been reported by Iloeje (1986) from the analysis of the data of South Devon and Zebu cattle. The phenotypic correlations were reported to be 0.94 and 0.92, respectively.

The estimate of the *genetic correlation* between birth weight and 200-day weight was 0.60 (TABLE 5.4). This positive and high estimate of the genetic correlation between birth weight and 200-day weight suggests that the genetic change in one trait is expected to accompany a change in the other. For example, selection for higher 200-day weights will increase birth weight as a correlated response, thus resulting in a higher incidence of calving difficulties.

The estimate of genetic correlation (0.60) between birth weight and 200-day weight as observed in the present study is close to the average of the published results (0.63) for birth weight and 200-day weight (TABLE

2.14). It is also close to the estimates of genetic correlation reported by Nelsen and Kress (1979), Winder et al.(1990) and Mackinnon et al.(1991) in different breeds of cattle. The estimates of genetic correlation as observed by these workers were 0.53 (Angus), 0.56 (Red Angus) and 0.57 (Zebu cross calves), respectively.

Slightly lower estimates of genetic correlation, 0.40 and 0.47, between birth weight and 200-day weight as compared to the present investigation were presented by Aaron et al.(1987) and Johnston et al.(1992a), respectively in Santa Gertrudis and Charolais cattle. Fahmy and Lalande (1973) and Iloeje (1986) reported genetic correlations between these two traits ranging between 0.77 and 0.83 in different breeds of beef cattle. Contrary to all these findings, Pabst et al.(1977) reported a low estimate of the genetic correlation (0.18) between birth weight and 200-day weight.

The *environmental correlation* between birth weight and 200-day weight was estimated to be 0.11 (TABLE 5.5). The environmental correlation between birth weight and 200-day weight as obtained in the present study was lower than the estimates reported in the literature (chapter 2). Winder et al.(1990) and Johnston et al.(1992a) had reported environmental correlations between the two traits of 0.25 and 0.32, respectively, higher than the estimates obtained in the present study.

The estimate of the *phenotypic correlation* between **birth weight and 400-day weight** as obtained in the present study was 0.19 (TABLE 5.3). It is almost half of the average phenotypic correlation (0.39) between birth weight and yearling weight compiled from the literature (TABLE 2.14). A low estimate of the phenotypic correlation (0.25) had also been reported by Pabst et al.(1977) from the analysis of the data of Hereford cattle. Winder et al.(1990), Mackinnon et al.(1991) and Johnston et al.(1992a), however,

found relatively higher estimates of the phenotypic correlation (0.35 to 0.39) in different breeds of beef cattle.

The estimate of the *genetic correlation* between birth weight and 400-day weight was 0.41 (TABLE 5.4). It may be concluded from this moderately high and significant ($P<0.01$) estimate of the genetic correlation that the same genes tend to influence the two traits and that selection for one will improve the other as a correlated response, i.e. higher birth weights will generally be associated with higher 400-day weights. This type of genetic correlation seems undesirable because selection for higher 400-day weights will increase birth weights and greater dystocia may result.

The estimate of genetic correlation between birth weight and 400-day weight of 0.41 is smaller than the average value of genetic correlation (0.56) from the results published in the literature (section 2.5.1) but the genetic correlation between these two traits had also been reported to be positive and moderately high by Mackinnon et al.(1991) and Johnston et al.(1992a). The genetic correlation between birth weight and 400-day weight was 0.47 in Zebu crosses as reported by Mackinnon et al.(1991) while the estimate reported by Johnston et al.(1992a) in Charolais cattle was o.46. The estimate of genetic correlation between birth weight and yearling weight was observed to be relatively high (0.57) in a study conducted by Winder et al.(1990) on data of Red Angus cattle. However, a positive but low estimate of the genetic correlation (0.26) was observed by Pabst et al.(1977) between birth weight and 400-day weight in Hereford cattle in UK.

The *environmental correlation* between birth weight and 400-day weight was 0.10 (TABLE 5.5), lower than the estimates reported in the literature (TABLE 2.14). Winder et al.(1990) and Johnston et al. (1992a), however, presented relatively high estimates of environmental correlation

between birth weight and 400-day weight. The estimates as reported by these workers were 0.25 (Red Angus) and 0.35 (Charolais), respectively.

The *phenotypic correlation* between **200-day weight and 400-day weight** was positive (0.79) and very high (TABLE 5.3). This is in agreement with the findings from the review of the pertinent literature (chapter 2). The average phenotypic correlation between the two traits was found to be 0.74 (TABLE 2.14). Positive and high estimates of phenotypic correlation between 200-day weight and 400-day weight ranging between 0.73 and 0.85 have also been reported by Kennedy and Henderson (1975b), Iloeje (1986) and Mackinnon et al.(1991) in different breeds of beef cattle. Mackinnon et al.(1991) analysed the 1267 performance records of Zebu cross cattle using bivariate REML animal model procedure. The phenotypic correlation between weaning weight and yearling weight (12 month weight) was estimated to be 0.76.

Slightly lower estimates of phenotypic correlation between 200-day weight and 400-day weight as compared to the estimate obtained in the present study had been reported by Blackwell et al.(1962), Pabst et al. (1977), Perez-Camara (1990), Winder et al.(1990) and Johnston et al. (1992a). The estimates of phenotypic correlation as observed by these workers ranged from 0.57 in Aberdeen Angus (Pabst et al.,1977) to 0.69 in Charolais cattle (Johnston et al.1992a). The performance records of 1418 progeny of 53 Charolais sires were analysed by Johnston et al.(1992a) using two trait REML (sire model) and the phenotypic correlation between 200-day adjusted weight and 365-day adjusted yearling weight was found to be 0.69. However, In Simmental cattle the phenotypic correlation between 200-day weight and 400-day weight was reported to be 0.63 by Perez-Camara (1990) using an animal model REML procedure.

The *genetic correlation* between 200-day weight and 400-day weight was estimated to be 0.96 (TABLE 5.4) and is in the upper tail of the literature estimates (TABLE 2.14). This very high estimate of the genetic correlation between 200-day weight and 400-day weight implies that any improvement in 200-day weight as a result of selective breeding will be expected to result in improvement in 400-day weights.

A very high estimate of genetic correlation between 200-day weight and 400-day weight was also reported by Perez-Camara (1990). The performance records of British Simmental cattle were analysed by Individual animal model restricted maximum likelihood procedure. The genetic correlation between 200-day weight and 400-day weight was noted to be 0.92. Schaeffer and Wilton (1981), however, observed a slightly lower estimate (0.63) of the genetic correlation from the analysis of the data of Canadian Simmentals as compared to the findings of the present study.
Very high estimates of genetic correlation (0.74-0.84) between weaning weight and yearling weight had also been reported by Kennedy and Henderson (1975b), Iloeje (1986), Winder et al.(1990) and Mackinnon et al.(1991). The performance records of Red Angus cattle were analysed by Winder et al.(1990). The genetic correlation between 205-day weight and 365-day weight was observed to be 0.78. Mackinnon et al.(1991) reported a genetic correlation of 0.84 between weaning weight and yearling weights of 1267 Zebu cross animals using bivariate animal model REML procedure.

The genetic correlation between 200-day weight and 400-day weight as obtained in the present study was much higher than the findings of Pabst et al.(1977) and Johnston et al.(1992a). The data of Devon, Hereford, Aberdeen-Angus and Sussex cattle collected in the pedigree recording scheme of the Meat and Livestock Commission of Britain were analysed by Pabst et al.(1977). The estimates of genetic correlation between 200-day

weight and 400-day weight were 0.68, 0.58, 0.38 and 0.37, respectively. In Charolais cattle the estimate of genetic correlation between 200-day adjusted weaning weight and 365-day adjusted yearling weight was observed to be moderate by Johnston et al.(1992a). The data of 1418 calves from 53 sires was analysed by REML sire model. The genetic correlation between these two traits was estimated to be 0.47.

The estimate of the *environmental correlation* between 200-day weight and 400-day weight revealed a trend similar to that exhibited by the phenotypic and genetic correlations between these two characters. The environmental correlation between 200-day weight and 400-day weight was estimated to be 0.68 (TABLE 5.5), close to the average estimate (0.66) from the published literature (TABLE 2.14). It implies from this high estimate of the environmental correlation that the environmental factors favouring 200-day weight have a desirable impact on 400-day weight.

The environmental correlation (0.68) as observed in the present investigation was in accordance with the findings of Kennedy and Henderson (1975b) and Johnston et al.(1992a). The performance records of 1418 Charolais cattle were analysed by Johnston et al.(1992a) utilising a REML sire model. The environmental correlation between 200-day adjusted weaning weight and 365-day adjusted yearling weight was reported to be 0.73.

Blackwell et al.(1962) observed a very high estimate of environmental correlation between weaning weight (weight when weaned at about 7 months of age) and yearling weights (weight on range at approximately 18 months of age) of Hereford (420 heifers and 499 steers combined data set) cattle. The performance records were analysed using paternal half-sib analysis of (co) variance procedure and the environmental correlation was 0.83. Perez-Camara (1990) and Winder et al.(1990)

reported lower estimates of environmental correlation between weaning weight and yearling weight in Simmental and Red Angus cattle as compared to the estimate of the present study. The performance data of 4461 Simmental cattle was analysed using individual animal model REML by Perez-camara (1990). The environmental correlation between 200-day weight and 400-day weight was estimated to be 0.48.

For the analysis of this bivariate combination there was a slight increase in the phenotypic variance of 400-day weight as compared to the corresponding estimate from the univariate analyses (from 1818 for the univariate analyses to 2020 for the bivariate analyses). To investigate the argument that animals having a 400-day weight record have been subject to some culling on the basis of their 200-day weight records and thus creating a bias in the genetic parameter estimates, the phenotypic selection differential (Falconer,1989) was calculated for 200-day weight. From the selection differential, the culling rate appeared to be of the order of 10 percent. It was also observed that if there had been a true truncation selection on the basis of 200-day weight the phenotypic variance for 400-day weight would have been reduced by a factor of 0.82. As the data used in the present study were obtained from commercial herds participating in the recording scheme of M.L.C., it is very difficult to exactly quantify the effects of selection exerted on the basis of 200-day weight because selection rules (criteria) of the individual farmers / breeders are not known from the field data. However, the effects of selection (if any) on the basis of 200-day weight seem to have been taken care of by the inclusion of all of the available 200-day weight records in the analysis.

It is seen that the estimates of the phenotypic correlation of birth weight with 200-day weight and 400-day weight were similar in direction but smaller in magnitude than their genetic counterparts. The phenotypic correlation of 200-day weight with 400-day weight was also lower than the respective genetic correlation. This finding is in agreement with the review of the literature in chapter 2.

The discrepancy between phenotypic and genetic correlations of birth weight with other performance traits was more noticeable. The approximate standard errors of the estimates of genetic correlations were calculated following the procedures outlined by Falconer (1989). It was found that the standard errors were very low for genetic correlations among the weight traits and indeed between other pairs of highly correlated traits, for example, 400-day weight and muscling score. For birth weight with 200-day weight and 400-day weight, the estimates of the standard errors of the genetic correlations were 0.03 and 0.05, respectively. It, therefore, seems that the discrepancy among the phenotypic and genetic correlations of birth weight with other performance traits is real because of the low estimates of the standard errors of the genetic correlations.

Although we can not presently identify the cause of this difference, the possible continued presence of some "standard" birth weights in the data may contribute to this. Also, the incorporation of maternal effects into the bivariate analyses might change the relative sizes of the genetic and environmental correlations, just as the incorporation of maternal effects into the univariate analyses changed the heritabilities.

combinations is also similar to the relationship of 200-day weight with 400-day weight.

The estimate of *phenotypic correlation* between **preweaning gain and postweaning gain** in the present study was 0.17 (TABLE 5.6). Similar value of phenotypic correlation (0.19) was reported by Bourdon and Brinks (1982) for the males while the corresponding estimate for the females was –0.10.

The weight gain in the preweaning period appears to be highly genetically correlated with the weight gain in the postweaning period, the *genetic correlation* being 0.82 (TABLE 5.7). This suggests that weight gains before and after weaning are controlled by the same genes and selection for example for increased preweaning gain will automatically improve the postweaning gains. The published results concerning the genetic correlation between preweaning gain and postweaning gain are highly variable. Brinks et al.(1964), for example, presented low and negative (–0.23) estimate of the genetic correlation between these two traits from the analysis of 3584 records of Hereford heifers while Bourdon and Brinks (1982) observed a positive and moderately high estimate (0.56) of the genetic correlation between preweaning gain and the postweaning gain for males and a low positive estimate (0.09) for the females.

The *environmental correlation* between preweaning gain and postweaning gain was –0.03 (TABLE 5.8). Negative but relatively high estimates of the environmental correlation between these two traits are reported by Brinks et al.(1964) for Herefords (heifers,–0.23) and by Bourdon and Brinks (1982) for Red Angus, Hereford and Angus cattle (–0.24 in males and –0.31 in females).

The *phenotypic correlation* between **postweaning gain and postnatal gain** of 0.69 (TABLE 5.6) is close to the estimate of phenotypic

correlation (0.61) reported by Bourdon and Brinks(1982) for the female data and is smaller than the corresponding value (0.80) for males. Higher estimates of phenotypic correlation between postweaning gain and postnatal gain have also been reported by Alenda and Martin (1987) for Angus cattle (0.79 in males and 0.80 in females).

The *genetic correlation* estimate between postweaning gain and postnatal gain was 0.73 (TABLE 5.7). This estimate of the genetic correlation between preweaning gain and postnatal gain is high because of the part-whole relationship between the two traits.

Bourdon and Brinks (1982) and Alenda and Martin (1987) also observed high estimates of genetic correlation between postweaning gain and postnatal gain ranging between 0.55 and 0.90 for different sexes in Red Angus, Angus and Hereford cattle.

The *environmental correlation* between postweaning gain and the postnatal gain was 0.70 (TABLE 5.8). This is in line with the estimates of environmental correlation of 0.70 in males and 0.73 in females reported by Bourdon and Brinks (1982).

The *phenotypic correlation* between **birth weight and preweaning gain** was 0.17 (TABLE 5.6). Low estimates of phenotypic correlation between birth weight and preweaning gain were also reported by Brinks et al.(1964) in Hereford heifers (0.23) and by Bourdon and Brinks (1982) in Red Angus, Angus and Hereford cattle (0.26 both in males and females).

The *genetic correlation* of birth weight with preweaning gain was 0.52 (TABLE 5.7). Similar estimates of genetic correlation (0.56 in males and 0.51 in females) between birth weight and preweaning gain has been reported by Bourdon and Brinks (1982) in their study. This is in agreement with the trend shown by the genetic correlation (0.60) of birth weight with

200-day weight (TABLE 5.4) as preweaning gain and 200-day weight are very highly correlated both genetically (genetic correlation = 1.00) and phenotypically (phenotypic correlation = 0.99). These findings are in agreement with those of Bourdon and Brinks (1982).

The estimate of *phenotypic correlation* between **birth weight and postnatal gain** was 0.11 (TABLE 5.6). This is lower than the estimates of phenotypic correlation between birth weight and postnatal gain from the published results. For example, the phenotypic correlation between birth weight and postnatal gain ranged between 0.26 and 0.32 for different sexes in different breeds of cattle (Bourdon and Brinks , 1982 and Alenda and Martin,1987).

The *genetic correlation* between birth weight and postnatal gain was 0.35 (TABLE 5.7). It indicates the same trend as is evident from the genetic correlation of birth weight with 400-day weight (genetic correlation=0.41). This is due to the fact that postnatal gain and 400-day weight are highly correlated (phenotypic, genetic and environmental correlations all close to 1) traits. Similar relationships between postnatal gain and birth weight and 400-day weight have been observed by Bourdon and Brinks (1982).

The *phenotypic correlation* between **birth weight and postweaning gain** was −0.04 (TABLE 5.6). Contrary to the present findings, the phenotypic correlations between birth weight and postweaning gain ranging from 0.11 to 0.27 have been reported by Brinks et al. (1964), Bourdon and Brinks (1982), Alenda and Martin (1987) and Winder et al. (1990) in different breeds of cattle. Winder et al.(1990) analysed the 41184 performance records of Red Angus cattle using paternal half-sib analysis of (co)variance technique and the phenotypic correlations between birth weight and postweaning gain was reported to be 0.19.

The *genetic correlation* between birth weight and postweaning gain was –0.25 (TABLE 5.7). It may be concluded from this negative estimate of the genetic correlation between birth weight and postweaning gain that the animals which gain less during the prenatal period (thus have smaller birth weights) have genes which result in higher postweaning gains. This type of relationship seems favourable because selection for reduced birth weight to minimise the incidence of dystocia may not have any ill effects on postweaning growth.

As for the phenotypic correlation, the estimate of the genetic correlation between birth weight and postweaning gain is also contradictory to the estimates (0.07 to 0.61) from the available literature (Brinks et al.,1964; Bourdon and Brinks,1982; Alenda and Martin,1987 and Winder et al.,1990).

The *environmental correlation* between birth weight and postweaning gain was 0.03 (TABLE 5.8). Low environmental correlation between birth weight and postweaning gain has also been reported by Winder et al.(1990) for Red Angus cattle.

The *phenotypic correlation* between **200-day weight and postweaning gain** was 0.16 (TABLE 5.6). This is in line with the phenotypic correlation estimate of 0.12 reported by Perez-Camara (1990) between 200-day weight and postweaning gain from the data of 4456 British Simmental calves analysed by the animal model REML procedures. Winder et al.(1990) also reported a low estimate of the phenotypic correlation (0.10) between weaning weight and postweaning gain for Red Angus cattle.

The *genetic correlation* between 200-day weight and postweaning gain was estimated to be 0.72 (TABLE 5.7). It suggests that the genes which result in higher weights at the age of 200 days are also responsible

for increased gains after weaning. A higher value (0.63) of this genetic correlation was also observed by Perez-Camara(1990) in his study on Simmental cattle. Winder et al.(1990), however, reported a low value of the genetic correlation between weaning weight and the postweaning gain. The estimate of genetic correlation as observed by these workers was 0.18 which is very low as compared to the estimate from the present study.

The *environmental correlation* between 200-day weight and postweaning gain was negative but very small (TABLE 5.8). Low but positive estimates of the environmental correlation between weaning weight and postweaning gain (0.001 and 0.05, respectively) were reported by Perez-Camara(1990) and Winder et al. (1990).

The *phenotypic correlation* between **400-day weight and postweaning gain** was 0.74 (TABLE 5.6). Higher estimates of the phenotypic correlation between postweaning gain and yearling weight have also been reported by Blackwell et al.(1962), Perez-Camara(1990) and Winder et al.(1990). The values of the phenotypic correlation as reported by these workers were 0.58, 0.80 and 0.74, respectively.

The *genetic correlation* between 400-day weight and postweaning gain of 0.89 (TABLE 5.7) is close to the estimates reported by Blackwell et al.(1962) and Perez-Camara(1990) in Hereford (0.84) and Simmental (0.85) cattle, respectively. Winder et al.(1990) also reported a high estimate (0.75) of the genetic correlation between these two traits. It can be inferred from this very high estimate of the genetic correlation between postweaning gain and 400-day weight that many similar genes are controlling the two traits and selection for higher postweaning gain will improve 400-day weights as well.

Like its phenotypic and genetic counterparts the *environmental correlation* between 400-day weight and postweaning gain was also high

(0.72). It is in accordance with the findings of Perez-Camara(1990) and Winder et al.(1990) They reported environmental correlations of 0.83 and 0.73, respectively.

5.3.2.3 Correlations between weight traits, weight gains and backfat depth

The *phenotypic correlation* between **birth weight and backfat depth** was estimated to be very low and was 0.05 (TABLE 5.3). It seems to suggest that birth weight and backfat depth around 400 days of age are two independent traits, not influenced by each other.

The *genetic correlation* between birth weight and backfat depth was 0.09 which was not significant statistically (TABLE 5.4). This positive and low genetic correlation indicated that the calves which have higher weights at birth have very few genes which tend to increase backfat thickness. Thus selection for reduced backfat thickness may not have any bearing on the body weights at birth of the calf. It seems logical to conclude that birth weight of the animal should give no indication of the leanness at 400 days of age.

The *environmental correlation* between birth weight and backfat depth was estimated to be 0.03 (TABLE 5.5). It implies from this very low environmental correlation between birth weight and backfat depth that the influence of the environmental factors affecting birth weights is very negligible on backfat depth.

The *phenotypic correlation* between **200-day weight and backfat depth** was 0.16 (TABLE 5.3). Low estimate of phenotypic correlation between weaning weight and backfat depth has also been reported by Lamb et al.(1990). The data from 824 Hereford bulls was analysed by restricted maximum likelihood technique accounting for the relationship among bulls (95 sires). The phenotypic correlation between

205-day weaning weight and ultrasonic backfat was reported to 0.19. Neely et al.(1982), however, presented a relatively high estimate of phenotypic correlation between 205-day weaning weight and sonoray fat thickness (ultra-sonic fat thickness over longissimus area muscle). The data from 578 Hereford bulls from 66 sires was analysed by paternal half-sib analysis and the phenotypic correlation between 205-day weaning weight and sonoray fat thickness was found to be 0.26.

The *genetic correlation* between 200-day weight and backfat depth was 0.22 (TABLE 5.4) which was significant ($P<0.05$). This positive and low genetic correlation between 200-day weight and backfat depth indicated that selection, for example, for higher 200-day weights would not necessarily result in a higher correlated increase in backfat depth, which is desirable. It may be inferred from this low genetic correlation that body weight at 200 days of age may not yield any reliable information about leanness of the animal at 400 days. Thus the animals with heavier weaning weights have very few genes which tend to increase backfat thickness.

Lamb et al.(1990) also found a low genetic correlation between 205-day weaning weight and ultrasonic backfat thickness at 365 days from the REML analysis of data of 824 Hereford bulls. The genetic correlation between these two traits was estimated to be 0.13.

On the contrary, Neely et al.(1982) observed a negative but very low (-0.01) estimate of the genetic correlation between 205-day weaning weight and sonoray fat thickness at 365 days of age.

The *environmental correlation* between 200-day weight and backfat depth was 0.12 (TABLE 5.5). This low environmental correlation between 200-day weight and backfat depth suggested that two traits i.e. 200-day weight and ultra-sonic backfat depth at approximately 400 days are affected by different types of environmental factors.

The relationship of preweaning gain with backfat depth in terms of phenotypic, genetic and environmental correlations is exactly similar to that described for 200-day weight and backfat depth. The values of the three correlations for the former are 0.16, 0.23 and 0.12, respectively (TABLE 5.9).

The *phenotypic correlation* between **400-day weight and backfat depth** was 0.19 (TABLE 5.3), which suggested a low association between these two traits. Mavrogenis et al.(1978), however, observed relatively higher estimate, 0.28, of the phenotypic correlation between final weight (weight at 365 days) and fat depth (fatness measured by an ultrasonic scanner over the longissimus muscle) from data on individually fed Hereford bulls. The estimate of phenotypic correlation between 365-day weight and fat scan (Sonoray fat thickness) was reported to be 0.29 by Neely et al.(1982) in their study.

The *genetic correlation* between 400-day weight and backfat thickness was estimated to be 0.14 (TABLE 5.4) which was non significant ($p>0.05$). This low estimate of the genetic correlation between 400-day weight and backfat depth suggested that selection to improve 400-day weights would not be accompanied by a very big increase in backfat depths or attempts to reduce backfat depth (approximately at 400 days) will not have any marked declining effect on body weight at 400 days. Thus this magnitude of the genetic correlation between 400-day weight and backfat depth seems desirable.

Robinson et al.(1992) also reported a low estimate of the genetic correlation between live weight and ultrasonic fat depth. The data of 9232 Angus, Hereford and Polled Hereford animals was analysed by individual animal model REML procedure. The estimates of the genetic correlation

between live weight (at 300-600 days) and rump fat and rib fat (recorded at 300-600 days) were 0.07 and 0.12, respectively.

Low but slightly higher estimates of the genetic correlation between 365-day weight and fat thickness as compared to the present study were presented by Mavrogenis et al .(1978) and Neely et al.(1982). The genetic correlations between 365-day weight and fat depth were reported to be 0.29 and 0.19, respectively.

The *environmental correlation* between 400-day weight and backfat depth was 0.22 (TABLE 5.5). This low estimate of the environmental correlation between 400-day weight and backfat depth suggested that these two traits are not greatly influenced by similar environmental factors. As the estimate is positive and moderately low, it may be inferred that environmental factors having favourable effects on 400-day weight will also result in slight increase in backfat depth.

Moderate and relatively higher estimate of environmental correlation between live weight and backfat depth (0.34 between live weight and rump fat and rib fat) was reported by Robinson et al.(1992) for Angus, Hereford and Polled Hereford cattle.

The phenotypic, genetic and environmental correlations of postnatal gain with backfat depth are similar to those described above for 400-day weight and backfat depth (TABLE 5.9).

The relationship between backfat depth and postweaning gain in terms of phenotypic (0.12), genetic (–0.04) and environmental (0.16) correlations (TABLE 5.9) is very similar to that observed between backfat depth and weight traits and preweaning and postnatal gains.

5.3.2.4 Correlations between weight traits, weight gains and muscling score

The *phenotypic correlation* between **birth weight and muscling score** was 0.10 (TABLE 5.3). Information of similar type on the phenotypic relationship between birth weight and muscling score from the analysis of a combined sexes dataset is scanty in the available literature. Renand(1985), however, observed a phenotypic correlation of almost similar magnitude between birth weight and final fleshiness (skeletal size score at the end of fattening) from the analysis of data of the 699 male progeny of Charolais sires. The estimate of phenotypic correlation was found to be 0.08.

The *genetic correlation* between birth weight and muscling score was 0.39 (TABLE 5.4). The moderate estimate of genetic correlation between birth weight and muscling score as found in the present investigation suggested that there will be a correlated change in one trait as a result of selection for the other trait. It can be concluded that body weight at birth could be a reasonably good indicator of muscling around 400 days of age.

A similar estimate of genetic correlation (0.38) between birth weight and final fleshiness scores was reported by Renand(1985). Lower estimates of genetic correlation between birth weight and muscling scores of Hereford cattle were observed by Buchanan et al.(1982), 0.18 and 0.12 for bull and heifer datasets , respectively. Birth weight was also found to be lowly genetically correlated (0.16) with muscling score by Koch (1978) from the analysis of the data of 377 Hereford heifers.

The *environmental correlation* between birth weight and muscling score was estimated to be negative (0.03) and very low (TABLE 5.5). Buchanan et al.(1982), however, observed positive but low environmental correlations between birth weight and muscling score in Hereford cattle.

The estimates of environmental correlation as reported by Buchanan et al.(1982) were 0.10 and 0.05 in males and females, respectively.

The *phenotypic correlation* between **200-day weight and muscling score** was observed to be 0.40 (TABLE 5.3). A positive but relatively low estimate of the phenotypic correlation between weaning weight and final muscling (on a scale 0 to 17, recorded just prior to slaughter) was reported by Dinkel and Busch(1973) from the analysis of the data of 341 grade Hereford steers. The estimate of phenotypic correlation was found to be 0.21. Renand(1985) also presented a positive and very low estimate of the phenotypic correlation (0.03) between weaning weight and final fleshiness of the progeny of the Charolais sires.

On the contrary Blackwell et al.(1962) found negative and very low estimates of the phenotypic correlation between weaning weight and yearling grade (subjective appraisal of the type and conformation of the animal at approximately one year after weaning) . Blackwell et al.(1962) analysed the data of 499 steers and 420 heifers by paternal half-sib analysis of (co)variance. The estimates of phenotypic correlation between these two traits were −0.02, −0.15 and −0.07 in steers, heifers and combined dataset, respectively.

The *genetic correlation* between 200-day weight and muscling score was 0.43 (TABLE 5.4). This moderate genetic correlation estimate between 200-day weight and muscling score was statistically significant ($P<0.01$) and suggested that these two traits are influenced by many of the same genes and thus higher 200-day weights may be associated with higher muscling scores at the age of 400 days. A very similar genetic correlation estimate (0.38) between weaning weight and final fleshiness was reported by Dinkel and Busch (1973) for grade Hereford steers. Buchanan et al.(1982), however, obtained a negative and low (−0.24)

estimate of the genetic correlation between weaning weight and muscling score in Hereford bulls while in heifers the genetic correlation reported was 0.21. Negative and low genetic correlation estimates were also observed by Koch (1978) and Renand (1985) from the studies undertaken on Hereford females(–0.07) and Charolais bulls (–0.04), respectively. Negative and high values of genetic correlation between weaning weight and yearling grade (–0.48,–0.68 and –0.56 in steers, heifers and combined datasets, respectively) were presented by Blackwell et al.(1962).

The *environmental correlation* between 200-day weight and muscling score was 0.39 (TABLE 5.5). This moderate estimate of environmental correlation suggested that the environmental factors favouring 200-day weights had a desirable influence on muscling scores around 400 days of age. This is in agreement with the moderate estimates of environmental correlation (0.35 in bulls and 0.36 in heifers) between weaning weight and muscling score reported by Buchanan et al.(1982).

Contrary to these findings Blackwell et al.(1962) estimated low environmental correlations between weaning weight and yearling grade from the analysis of the data of Hereford steers and heifers. The environmental correlations were reported to be 0.09, 0.10 and 0.10 in steers, heifers and combined sexes datasets, respectively.

The phenotypic, genetic and environmental correlations between preweaning gain and muscling score are similar to those between 200-day weight and muscling score (TABLE 5.9).

The estimate of *phenotypic correlation* between **400-day weight and muscling score** was 0.42 (TABLE 5.3) suggesting thereby a moderate association between these two traits. Blackwell et al.(1962), however, reported quite variable results for different sexes as far as phenotypic correlation between yearling weight and yearling grade is

concerned. The phenotypic correlations were estimated to be 0.27 in steers, −0.12 in heifers and −0.01 for combined datasets. Renand and Gillard (1982) observed a phenotypic correlation of 0.27 between 365-day weight and muscle conformation scores of 699 bulls, the progeny of 39 Charolais sires.

The *genetic correlation* between 400-day weight and muscling score was observed to be 0.44 (TABLE 5.4) which was significant ($P<0.01$). This moderately high estimate of the genetic correlation between 400-day weight and muscling score suggests that selection for one trait will improve the other as a correlated response. We may say that higher muscling scores at approximately 400 days will be associated with higher body weights at this age.

The genetic correlation between 400-day weight and muscling score as obtained in the present study was much higher than the estimate reported by Robinson et al.(1992). The data of 3870 Angus and Hereford cattle were analysed by individual animal model REML. The estimate of the genetic correlation between live weight (at 300-600 days) and muscling score (subjective muscling score recorded at 300-600 days using a 15 category scale, represented by the numerical values 10,20,...150) was found to be 0.11 which is lower than the estimate of the present study.

Blackwell et al.(1962), however, reported negative and very high estimate of the genetic correlation between yearling weight and yearling grade. The estimates of the genetic correlation between the two traits were −0.66 in steers, −0.77 in heifers and −0.66 for combined datasets. Koch (1978) also reported a negative estimate (−0.19) of the genetic correlation between yearling weight and muscling score from the paternal half-sib analysis of (co) variance of the performance records of 377 Hereford heifers. Buchanan et al.(1982), however, obtained a negative and low

estimate (–0.14) in Hereford bulls and a low positive estimate (0.04) in the heifers.

The *environmental correlation* between 400-day weight and muscling score was 0.42 (TABLE 5.5) . It implies from this moderate estimate of the environmental correlation between 400-day weight and muscling score that the two traits are influenced by similar type of environmental factors (i.e. feeding and management etc.). Thus the environmental influences that result in higher body weights at 400 days have a desirable impact on subjective muscling scores.

Moderate estimates of the environmental correlation between yearling weight and yearling grade of Herefords (0.27 in steers, 0.58 in heifers and 0.35 for combined datasets) have also been reported by Blackwell et al.(1962). The environmental correlations between yearling weight and muscling score was relatively high (0.56) for Hereford bulls and heifers (Buchannan et al.,1982).

Robinson et al.(1992) reported a moderate estimate of the environmental correlation between live weight and muscling scores from Angus and Hereford herds. The data of 3870 animals was analysed by animal model REML technique and the estimate of the environmental correlation between live weight and muscling score was found to be 0.29.

The findings of the present study concerning the relationship between postnatal gain and muscling score expressed in terms of phenotypic (0.41), genetic (0.40) and environmental (0.42) correlations (TABLE 5.9) are similar to those observed between 400-day weight and muscling score.

The phenotypic, genetic and environmental correlations between postweaning gain and muscling score were 0.18, 0.17 and 0.18, respectively.

5.3.2.5 Correlations between backfat depth and muscling score

The estimate of the *phenotypic correlation* between backfat depth and muscling score was 0.15 (TABLE 5.3). It suggested that there is a low association between these two traits. Dinkel and Busch (1973), however, reported a negative but low estimate of the phenotypic correlation between fat depth and muscling scores (on a scale 0 to 17 recorded prior to slaughter) of grade Hereford steers. The phenotypic correlation between these two traits was estimated to be –0.09.

The *genetic correlation* between backfat depth and muscling score as obtained from the individual animal model restricted maximum likelihood analysis was 0.10 (TABLE 5.4) which was non significant ($p>0.05$). This low estimate of the genetic correlation between backfat depth and muscling score indicated that probably the two traits are affected by different genes. Generally the two traits appear to be independent of each other. Thus selection for decreased backfat depth may not have any marked adverse effect on muscling score and vice versa.

Robinson et al.(1992) also observed a low positive genetic correlation between fat depth and muscling score. The data of 3870 Angus and Hereford cattle aged 300-600 days at the time of scanning was analysed by individual animal model REML. The estimates of genetic correlation between ultrasonic rib fat and rump fat with muscling score (recorded on a 15 category scale, represented by the numerical values 10,20,...150) were found to be 0.11 and 0.05, respectively.

On the contrary, Dinkel and Busch (1973) reported a negative and moderately high estimate of the genetic correlation between fat depth and muscling score in their study. The genetic correlation as estimated by these workers was –0.46.

The *environmental correlation* between backfat depth and muscling score was positive but very low (TABLE 5.5). It implies that the environmental factors with a desirable effect, for example, on muscling score have very little to do with backfat depth and vice versa.

The estimates of environmental correlation between fat depth and muscling score (i.e. rump fat and muscling score, 0.09 and rib fat and muscling score, 0.11) as reported by Robinson et al.(1992) were almost close to that observed in the present study (0.17).

A very wide variation in the estimates of the phenotypic and genetic and environmental correlations between muscling score and other performance traits may be attributed to the subjective nature of the muscling score and the differences in the ages at measurement besides other factors.

5.4 Conclusions

Restricted maximum likelihood individual animal model bivariate analyses for the estimation of phenotypic, genetic and environmental parameters for various performance traits indicated that the estimates of heritability for weight traits, backfat depth and muscling score were very similar to the corresponding estimates from the univariate analyses (chapter 4). On the whole, the bivariate parameter estimates for weight traits agreed well with the literature estimates obtained elsewhere (chapter 2). The weight gains appeared to be moderately heritable with the exception of postweaning gain for which a low estimate of heritability was observed. The estimates of genetic correlation among weight traits were moderate to very high (0.60, for birth weight and 200-day weight ; 0.41, for birth weight and 400-day weight; 0.96, for 200-day weight and 400-day weight). These moderate to very high estimates of genetic correlations demonstrated that

selection for higher 200-day weight or 400-day weight would increase body weight at birth as a result of correlated response thus resulting in increased incidence of calving difficulties and reduced calf survival.

The genetic correlations among weight gains and between weight traits and preweaning gain and postnatal gain are also positive and moderate to very high. Some of these genetic correlations, e.g. between preweaning gain and postnatal gain or between postweaning gain and postnatal gain are high because of the part-whole relationships. The genetic correlations of postweaning gain with 200-day weight and 400-day weight were also very high. The relationship between birth weight and postweaning gain in terms of genetic correlation (–0.25) appeared to be most interesting. It suggested that small birth weights may be associated with higher postweaning gains.

The investigation of the relationship between weight traits and ultrasonic backfat depth revealed that there exists a very weak association between the traits of the two categories. This agrees well with the observations made from the review of the literature (chapter 2). The genetic correlations of backfat depth with birth weight, 200-day weight and 400-day weight were 0.09, 0.22 and 0.14, respectively. Almost the same estimates of genetic correlations were observed between weight gains and backfat depth. This low magnitude of the relationship is favourable because selection for improved growth rate at any stage will not result in a marked increase in backfat depth. So carcass quality as regards the leanness will not be affected much.

The other important and interesting result from the present investigation is the establishment of the relationship between weight traits, weight gains and muscling score based on large sized datasets using best available analytical procedures. The review of literature in chapter 2

suggested very variable and confusing results about the relationship of weight traits and conformation/muscling score. The present study has been successful in establishing the relationship between growth traits and muscling score. The genetic correlations of muscling score with birth weight, 200-day weight and 400-day weight were 0.39, 0.43 and 0.44, respectively. It implies that body weight at earlier periods of the animals' life may be used as reliable indicators of type and conformation at approximately 400 days of age. Preweaning gain and postnatal gain also had moderate estimates of the genetic correlations (0.44 and 0.40, respectively) with muscling score. Surprisingly postweaning gain appeared to be lowly genetically correlated with muscling score.

Backfat depth had a positive but very low estimate (0.10) of the genetic correlation with muscling score.

Multivariate individual animal model REML procedures are computationally very demanding, so that only small datasets and only few traits can be considered at the same time. Under the constraint of computational feasibility, it was not practicable to do a multivariate analyses with more than two traits considered simultaneously. Hence selection effects are not fully taken into consideration. It was also not feasible to fit models including maternal effects because of the large sized datasets involved and highly demanding nature of the analyses in terms of memory and time. Thus these two points require further research efforts as far as multivariate estimation of the genetic parameters is concerned.

CHAPTER 6

GENERAL DISCUSSION AND IMPLICATIONS

Accurate estimates of genetic parameters are important both for the evaluation and comparison of alternative breeding plans and the prediction of breeding values. The principal aims of this investigation were to estimate the phenotypic and genetic parameters of various performance traits of Simmental cattle in the UK herds and to explore the amount of variation due to maternal effects on the performance of these animals.

The univariate estimates of parameters (chapter 4) in the present study are obtained using the REML individual animal model with and without maternal effects. There are several points of interest as far as the univariate estimates of genetic parameters are concerned. Firstly, estimates of direct heritability for various weight traits are of moderate size ranging from 0.25 for birth weight to 0.35 for 400-day weight, indicating moderate genetic variation for these performance traits in British Simmental cattle.

Secondly, the maternal additive genetic effects are of nearly similar magnitude (4 to 6 percent of the phenotypic variation) for the three weight traits, i.e. birth weight, 200-day weight and 400-day weight whilst maternal permanent environmental effects expressed as a percentage of the phenotypic variance appear to decrease with age: 7 percent for birth weight, 5 percent for 200-day weight and 3 percent for 400-day weight.

Thirdly, the correlation between direct additive genetic and maternal additive genetic effects (r_{AM}) was negative in all cases. It showed a wide variation from −0.14 for 200-day weight to −0.45 for birth weight. Baker (1980) has indicated that the values of this genetic correlation may be

influenced by the negative environmental covariance between dam and offspring (see section 4.4 for details). More recently, Robinson (1994) has demonstrated that the estimates of r_{AM} may be negative not only because of the antagonism between direct additive genetic and maternal additive genetic effects but also because of the additional sire x year variation and negative dam-offspring covariances. The simulation study conducted by Robinson (1994) revealed that additional sire x year variation equivalent to 6 percent of the phenotypic variation resulted in negative r_{AM} estimates of approximately 0.50. Similar results were observed for data generated with a dam-offspring regression coefficient of –0.2. Therefore, additional sire x year variation and negative dam-offspring environmental covariance (both usually assumed to be absent in the currently available analytical techniques) are possible sources of bias in the estimation of r_{AM}.

The results of the present study concerning evaluation of maternal effects on the weight traits suggest that the direct additive genetic variation is higher than the total variation due to maternal effects. Thus the genetic makeup of the calf is more important in influencing weight traits than the prenatal (uterine environment) and postnatal (milking and mothering ability) maternal contributions. Maternal effects declined in importance as the animal grew older. This supports the argument that maternal effects are usually most evident for juvenile traits, but there may be some carryover effects for traits expressed later in life, at least to pre-adult stages of development.

For backfat depth and muscling score the inclusion of maternal effects, both genetic and environmental, into the models of analyses did not result in significant improvement in the log likelihood over the simple animal model. Thus it seems that there is little evidence to support the hypothesis that live animal traits, i.e. backfat depth and muscling score, are affected by maternal effects. This finding may not be general and it must be interpreted

with some care, as in the current investigation the quantity and quality of the datasets for these two traits limited the proper disentanglement of the direct and maternal contributions from the dam. However, the results do suggest that there is a moderate direct genetic variation for both of these traits.

Many noteworthy results have emerged from the multivariate (bivariate) individual animal model REML analyses (chapter 5). For instance, all weight traits, preweaning gain and postnatal gain appear to have moderate estimates of heritability while for postweaning gain, surprisingly, a low value is observed. The only possible explanation for this small estimate seems that selection on the basis of 200-day weight might have created a downward bias in the heritability estimate for postweaning gain, but it is not very easy to quantify such effects because the selection criteria of the individual breeders are not known from the field records.

The other important point to note is that there is a positive and moderate to very strong genetic relationship among body weights at birth, 200 days and 400 days of age as expected, as there is a part-whole relationship between these weight traits. Thus selection for any one of these traits is likely to be accompanied by a positive correlated change in the other unselected traits, so selection on later weights will result in higher birth weights and potentially undesirable effects on the ease of calving. If selection is aimed at decreasing birth weights exclusively to reduce calving difficulties, rapid progress would be expected. However, this will result in serious declines in other weight traits.

The genetic correlations among weight gains and between weight traits and preweaning gain and postnatal gain are also positive and moderate to very high.The estimates of genetic correlation of postweaning gain with other weight traits follow the same trend as is observed for preweaning gain and postnatal gain with weight traits with the exception of a notable genetic

relationship with birth weight (genetic correlation being –0.25). The negative genetic association between birth weight and postweaning gain suggests that selection for reduced birth weights to avoid dystocia may not have a detrimental effect on postweaning growth. A possible explanation for this type of relationship may be that the calves which have stunted prenatal growth (smaller birth weights) undergo some sort of compensatory growth during the postweaning period.

In order to minimise the effects of selection for weight on birth weight, one approach may be to direct selection towards weights at later ages such as 400-day weight as the value of genetic correlation between birth weight and 400-day weight is far from unity (0.41). Thus it appears biologically feasible to increase 400-day weight with little change in birth weight. Lighter birth weight is associated with a shorter gestation period. Direct selection for shorter gestations seems unfeasible under the extensive beef production system, where breeding dates are seldom recorded. So selection for smaller birth weights and heavier 400-day weights primarily among the bulls should result in gradual reduction of gestation periods, permitting more rapid prenatal growth without disturbing calving ease (Dickerson et al.1974). But this type of solution to the problem may not be applicable to all beef production systems as this is expected to lead to increased mature weights and thus greater maintenance requirements and in some cases to reduced fertility, which seems contradictory to the selection objectives for the suckler herds. In suckler herds small to medium sized cows are usually considered desirable because of their lower maintenance requirements (even though calves from such cows usually tend to be smaller). Moreover, the preponderance of evidence suggests that the incidence of calving difficulties is lower in small to medium sized cows than the large ones.

Selection for weight gain rather than total weight as a means of avoiding unwanted correlated changes in birth weight while maintaining a high rate of response in other growth traits seems a better solution to the problem (Koch et al.,1974). In this respect postnatal gain as a selection criterion offers a lot of promise because the genetic correlation between birth weight and postnatal gain is a little smaller (0.35) than that between birth weight and 400-day weight (0.41). Moreover, it is positively highly genetically correlated with other weight traits and gains, with a moderate heritability. Thus it is expected to respond to selection.

As a selection criterion for successful beef production weight of the calf weaned (200-day weight) has its own merits. For example, 200-day weaning weight includes measures of production and fertility of the cow, it is an easy trait to measure with a moderate heritability (0.26 from the maternal effect model) and it has a positive and very strong genetic relationship with 400-day weight thus giving some good indication of the animal's genetic potential for future growth at a younger age. Selection for 200-day weaning weight (being a composite trait) should result not only in some positive response in the calf's ability to grow but also in the dam's capability to provide a maternal environment for that growth. Most studies concerning the correlation between direct additive genetic and maternal additive genetic effects are still inconclusive; so if the true value of this correlation is positive, then such selection should improve both direct additive genetic and maternal additive genetic components. Although the estimate of this direct-maternal genetic correlation obtained in the present study is slightly negative (–0.14), it is not significantly different from zero.

Selection indices with restriction on birth weight have been suggested (for example, Simm et al.,1986) to have a combined selection for efficient beef production and to prevent economic losses due to calving difficulties.

The other important result from the bivariate animal model REML analyses is the finding that a weak genetic association exists between backfat depth and weights and weight gains. Thus selection for improved growth is not expected to have a major influence on subcutaneous fat (as measured by ultrasonic scanner) and hence on carcass quality. Therefore, higher body weights can give reliable indications of saleable meat yield and more returns to the farmers / producers.

A positive and moderate genetic relationship was found between weight traits and muscling score as would be expected, such that larger animals are associated with higher muscling scores. However, estimates from the literature ranged widely from negative to positive (TABLE 2.15). The genetic correlations between weight gains and muscling score are also of similar magnitude and direction except that between postweaning gain and muscling score which is low. The explanation of this unexpected relationship is not very clear.

For Simmental cattle as a terminal sire breed, selection for growth rate and leanness still has a lot of scope as was indicated by Barlow (1984) sometime ago, but for suckler herds of Simmental and other maternal breeds reared as purebred or crossbred, selection for growth traits (direct effects) does not appear to have a very strong relationship with efficiency of production (Barlow,1984), indicating the need for seeking new selection criteria. Further investigations are needed to examine alternative selection criteria to improve efficiency of beef production. The data here in the present study relate only to growth and not to feed efficiency, an important objective particularly in intensive feeding conditions.

Measurement of carcass traits on the live animal has been advocated by many workers. For example Robinson et al.(1993) say that the importance of carcass traits to the beef cattle industry is increasing, especially with the

introduction of more detailed carcass specification systems and the payment of premiums for products satisfying the requirements of specific markets. The ability to measure carcass traits on the breeding animals is advantageous because it avoids the delay and expense of progeny testing. Moreover, genetic evaluation by mixed model methodology makes it possible to estimate breeding values using information from young animals and all relatives and related traits. Live animal measurement by ultrasound for subcutaneous fat depth has been shown to be at least as accurate as measurements on the carcass (Robinson et al.,1992) while ultrasonic measurement of longissimus muscle area is marginally less accurate than careful carcass measurements. Robinson et al.(1993) estimated genetic parameters for ultrasonic fat depths (rib and rump), longissimus muscle area and muscle score. Results indicated that carcass traits measured by ultrasound and predictions of meat yield are moderately heritable and that genetic progress based on genetic evaluations by mixed model analysis can be made. Similar results were obtained in the present study as far as the heritability of ultrasonic backfat depth is concerned.

McGuirk et al.(1994) highlighted the need for considering calving ease and calf quality as important selection criteria for beef bulls used for crossing in dairy herds. They indicated that calving difficulty inflicts substantial economic losses and has very important implications for the dairy herds. Calving difficulties not only pose a risk to the survival of cow and calf but also adversely affect productive and reproductive performance. This leads to increased culling rate as a consequence. As regards the calf quality, it was pointed out that a high proportion of crossbred dairy calves are sold soon after birth (generally at less than 3 weeks of age). At major auction centres in England and Wales, an important price differential (average for 1993 for all breeds was £ 56) between first and second quality calves under 3 weeks of

age has been observed (McGuirk et al., 1994). Thus calving ease and calf quality are important economic traits for dairy herds especially for those using continental beef breeds like the Simmental, Charolais and Limousin as terminal sires.

Tier and Graser (1994) suggested that the identification and definition of all traits of economic interest should be the first and important task in the development of any genetic evaluation system. The end product of the beef industry is not simply meat but meat of defined quality produced at the least possible cost. They are of the view that the high maintenance cost and low reproductive rate of cows make mature size/weight and fertility traits very important for efficient beef production. Fertility traits may include age at first oestrus, age at first calving, pregnancy test results, calving success / failures, calving ease, calving interval, non return to first service, number of services per gestation etc. The use and consideration of these reproduction traits in beef evaluation is problematic as they are lowly heritable and their recording is either difficult or expensive. Moreover the analysis of some of these traits (threshold characters, e.g. calving ease) is not very simple. Tier and Graser emphasise that traits relating to structural soundness may be very important to beef breeders, so that breeding animals can perform efficiently throughout their lifetime, whilst traits such as disease, parasite resistance or temperament affecting the health and welfare of both the animals meant for breeding and slaughter, may be important for some breeds and some production systems.

Currently in Britain the evaluations of beef cattle are being carried out using multi - trait individual animal model BLUP procedures with parameters estimates pooled from the literature (TABLE 6.1). The phenotypic, genetic and environmental parameters obtained in the present study should be more reliable as datasets were large and the best currently available analytical

TABLE 6.1 Estimates of phenotypic and genetic parameters for various performance traits already in use by Meat and Livestock Commission for beef cattle evaluations in Britain (Crump et al.,1994).

Traits	Bwt direct (kg)	200 wt direct (kg)	400 wt direct (kg)	Fd direct (mm)	Ms direct (points)	Bwt maternal (kg)	200 wt maternal (kg)	400 wt maternal (kg)
Bwt[a] direct[b]	0.41	0.49	0.53	0.00	0.00	–0.38	-	-
200 wt direct	0.35	0.28	0.82	0.00	0.00	-	–0.32	-
400 wt direct	0.38	0.72	0.41	0.21	0.10	-	-	0.00
Fd direct	0.00	0.24	0.36	0.29	0.00	-	-	-
Ms direct	0.00	0.10	0.30	0.10	0.25	-	-	-
Bwt maternal	-	-	-	-	-	0.06	-	-
200 wt maternal	-	-	-	-	-	-	0.07	-
400wt maternal	-	-	-	-	-	-	-	0.00

Heritability estimates on the diagonal, genetic correlations above the diagonal, phenotypic correlations below the diagonal. The estimates of maternal permanent environmental effects as a proportion of the phenotypic variance used are 0.06 for birth weight and 0.08 for 200-day weight.

[a]Bwt, birth weight; 200wt,200-day weight; 400wt,400-day weight; Fd, backfat depth; Ms, muscling score.

[b]direct, direct additive genetic effects; maternal, maternal additive genetic effects.

procedures (individual animal model REML) were used. The various phenotypic, genetic and environmental parameters recommended as a result of the present investigation are presented in TABLE 6.2. These estimates of parameters will provide a bench mark for British beef cattle population and their use should not only improve the credibility of the animal evaluations in the UK but also lead to more accurate selection and estimation of the response. At present beef cattle evaluations consider maternal effects only for birth weight and 200-day weight. The analysis of the data for 400-day weight revealed that maternal effects accounted for about 7 percent (4 percent for maternal additive genetic and 3 percent for maternal permanent environmental effects) of the phenotypic variation with a negative direct-maternal genetic correlation of –0.27. Thus it is suggested from the findings of the present study that BLUP evaluations should also include maternal effects for 400-day weight.

Different areas which require further investigations as regards the estimation of genetic parameters can be identified. Firstly, for univariate analyses more research is needed to allow the fitting of models involving the correlation between direct additive genetic and maternal additive genetic effects, sire x herd interactions and dam-offspring correlations in sets of data that are sufficiently large to allow these effects to be disentangled and to have more realistic predictions of the genetic merit of the animals.

Secondly, the presence of grand-maternal effects, non-additive genetic effects (Willham, 1972) and non-nuclear cytoplasmic maternal genetic effects has been argued by several workers (for example, Tess et al.,1987). In the case of non-nuclear maternal genetic effects mitochondria are thought to be the possible sources of variation, as they contain DNA and are inherited through the dam. Thus the usual genetic effects of nuclear

TABLE 6.2 Estimates of phenotypic and genetic parameters for various performance traits obtained in the present study

Traits	Bwt direct (kg)	200 wt direct (kg)	400 wt direct (kg)	Fd direct (mm)	Ms direct (points)	Bwt maternal (kg)	200 wt maternal (kg)	400 wt maternal (kg)
Bwt[a] direct[b]	0.25	0.60	0.41	0.09	0.39	−0.45	-	-
200 wt direct	0.28	0.26	0.96	0.22	0.43	-	−0.14	-
400 wt direct	0.19	0.79	0.35	0.14	0.44	-	-	−0.27
Fd direct	0.05	0.16	0.19	0.32	0.10	-	-	-
Ms direct	0.10	0.40	0.42	0.15	0.26	-	-	-
Bwt maternal	-	-	-	-	-	0.06	-	-
200 wt maternal	-	-	-	-	-	-	0.05	-
400wt maternal	-	-	-	-	-	-	-	0.04

Heritability estimates on the diagonal, genetic correlations above the diagonal, phenotypic correlations below the diagonal. The estimates of maternal permanent environmental effects as a proportion of the phenotypic variance are 0.07 for birth weight, 0.05 for 200-day weight and 0.03 for 400-day weight.

[a]Bwt, birth weight; 200wt,200-day weight; 400wt,400-day weight; Fd, backfat depth; Ms, muscling score.

[b]direct, direct additive genetic effects; maternal, maternal additive genetic effects.

origin are confounded with the cytoplasmic maternal effects. So there is a need not only to properly disentangle nuclear direct genetic effects and maternal genetic and maternal permanent environmental contributions but also to evaluate non-nuclear maternal genetic effects.

Thirdly, as regards the investigations of the relationships (both phenotypic and genetic) between various performance traits, it would be worthwhile to fit multivariate maternal animal models to account for the effects of selection and maternal effects, so as to have accurate estimates of the genetic parameters.

Fourthly, it will be interesting to investigate the mode of inheritance of and the relationship between fertility traits, growth and live animal measurements including ultrasonic backfat depth, muscle depth and visually assessed muscling score. The study of the nature of the relationship between growth traits and carcass quality traits may also be useful to produce the carcasses of the desired quality and standard to meet consumer demands.

The present study appears to be the first of its kind in the available literature which has been able to generate estimates of the genetic parameters with very large datasets using the individual animal model REML procedures. There have been some attempts in the past to estimate genetic parameters (for example, Meyer,1992; Swalve, 1992 and Waldron et al., 1993) using this methodology but either the size of the dataset used was small or parameters estimates were averaged over several sub datasets, so selection effects might not have been properly taken care of. The current investigation successfully has been able to extend the size of the population used in estimating parameters from an individual animal model. However, some points as listed above need further work to obtain better selection criteria for efficient beef cattle production.

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APPENDIX

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Animal Breeding Abstracts

Estimates of genetic and phenotypic parameters of some performance traits in beef cattle

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I. Abstract

This paper reviews the genetic and phenotypic parameters of birth, weaning and yearling weights, muscling score and ultrasonic fat depth of beef cattle, published worldwide. A summary is also given of estimates of genetic parameters due to maternal effects on these traits. The estimates of heritability (h^2) for birth, weaning and yearling weights (weighted by the number of observations) averaged 0.46, 0.39 and 0.24 for males, 0.26, 0.23 and 0.20 for females and 0.49, 0.48 and 0.41 across sexes. The corresponding values for muscling score and fat depth were 0.24 and 0.31, 0.28 and 0.24, and 0.57 (based on one study) and 0.33. Direct and maternal heritabilities averaged 0.30 and 0.10 respectively for birth weight, 0.22 and 0.13 for weaning weight and 0.31 and 0.11 for yearling weight, whilst permanent environmental variance as a proportion of the phenotypic variance (c^2) averaged 0.03, 0.07 and 0.03 respectively. The genetic correlation between direct and maternal effects averaged –0.35, –0.15 and –0.26 for the 3 traits respectively. The average repeatability estimates for birth and weaning weights (as traits of the dam) were 0.21 and 0.29 respectively in males (based on one study), 0.23 and 0.44 in females and 0.27 and 0.23 in combined sexes. The repeatability estimates for yearling weight (based on one study) were 0.21 in males and 0.48 in females. The genetic correlations (r_A) between birth weight and weaning weight averaged 0.47 in males, 0.41 in females and 0.63 in combined sexes, while those between birth weight and yearling weight were 0.64, 0.51 and 0.56 respectively. The average r_A between weaning weight and yearling weight was 0.88 in males, 0.76 in females and 0.76 in combined sexes. The growth traits do not seem to be highly genetically correlated with muscling score and ultrasonic fat depth.

I. Introduction

The potential for genetic change in economically important characteristics of domestic animals such as beef cattle depends to a large degree on the magnitude of the genetic variances and heritabilities of the characters considered in selection. The nature and extent of the relationships among traits are also involved in the genetic change effected by selection. Effective breeding plans are based on knowledge of the composition and relative importance of the genetic and environmental variation of a trait in the population under consideration.

The genetic parameters, which are functions of (co)variance components, provide information about the genetic nature of traits, and are needed to predict direct and correlated responses to selection, formulate selection indices and determine the method of selection. Estimates of these parameters are required for the mutiple-trait mixed model method for the prediction of breeding value. Preston and Willis (1970) reviewed genetic parameter estimates for various performance traits in beef cattle. The purpose of the present review is to update information on the amount of genetic and phenotypic (co)variation amongst various performance traits in beef cattle.

The growth traits of mammals are affected not only by their genetic makeup but also by the prenatal and postnatal environments provided by the dam, besides other environmental factors. Prior to weaning, the prenatal environment and the milking and mothering ability of the dam constitute an important part of

a young animal's environment. The expression of maternal ability in calf performance is confounded with the expression of genes for growth, half of which are received from the dam. Thus genetic variability for growth traits in mammals contains this additional complexity of maternal effects.

Knowledge of the kind and relative amount of genetic variation attributable to maternal effects, especially the sign and magnitude of the genetic correlation between direct and maternal effects of traits with high economic importance, is critical in the design of optimal breeding plans for most domestic mammals (Willham, 1980).

Thus, both direct and maternal effects should be taken into consideration to achieve optimum genetic gain in a selection programme. This is especially important if a negative covariance exists between these two effects. Baker (1980) and Robison (1981) have discussed the influence of maternal effects on the efficiency of selection in beef cattle. Meyer (1992) has presented some literature estimates of genetic parameters due to maternal effects on growth traits. In the present venture an attempt will also be made to thoroughly investigate the estimates of direct and maternal effects from the available literature in beef cattle.

III. Estimates and discussion

1. Heritability

Estimates of heritability (h^2) for various performance traits obtained by different procedures are not expected to be the same. This is due to the fact that different methods of estimation give values that contain different proportions of the non-additive genetic and environmental sources of variation. Most of the estimates of heritability for various performance traits (Tables 1, 2, 3 and 4) were computed using the correlation between paternal half-sibs. Carter and Kincaid (1959) pointed out that data must meet the following requirements in order for paternal half-sib correlation estimates to be accurate: (1) a large number of degrees of freedom for sires, (2) the absence of selection between sires, (3) the absence of environmental correlations between half-sibs, and (4) a large number of progeny per sire. Moreover, the assumptions of random mating, absence of epistatic effects and no covariance between genotype and environment must hold. The major advantage of using the paternal half-sib correlation to estimate h^2 is that this value contains only the additive plus a negligible fraction of the epistatic portion of the genotypic variance. In this method the intraclass correlation is multiplied by 4, since the average relationship among half-sibs is one-fourth. This method is limited by the fact that errors due to sampling or incorrect estimation of environmental influences are multiplied by 4.

With the availability of increased computing power, the use of restricted maximum likelihood (Patterson and Thompson, 1971) and animal models has become a standard practice in the analysis of animal breeding data throughout the world. This method has some unique attributes which have made it the method of choice. For example, it accounts for the loss in degrees of freedom due to fixed effects in the model; it is an iterative procedure well suited for use with mixed model equations along with the expectation maximization algorithm; it eliminates the bias due to selection; and it takes into account all the relationships present in the pedigree. This method appeals to animal breeders due to its well known asymptotic properties. Convergence in the parameter space is guaranteed if positive definite starting values are used (Henderson, 1984).

The estimates of h^2 for birth weight in various breeds are given in Table 1. They range from 0.09 in Holstein × zebu to 1.00 in Hereford cattle. The average estimates for males and females are 0.46 and 0.39 respectively, 0.24 being the average across sexes (Table 5).

The h^2 estimates for weaning weight are presented in Table 2. The average values of h^2 estimated for weaning weight are 0.26 in males, 0.23 in females, 0.27 in steers and 0.20 across sexes. Wide ranges were observed for h^2 estimates: from 0.06 to 0.63 in males, from 0.00 to 0.69 in females and from –0.13 to 0.84 in steers. Small and negative estimates of sire component h^2 (Rollins and Wagnon, 1956; Swiger *et al.*, 1962; Blackwell *et al.*, 1962; Massey and Benyshek, 1981) may be attributed to a small number of progeny per sire group, sampling error or genotype-environmental interaction, besides other factors. Gill and Jensen (1968) investigated the probability of obtaining negative estimates of h^2. They demonstrated that if the true h^2 is relatively low (0.1), at least 800 observations are necessary for a 95% chance of obtaining a non-negative estimate from the sire component of variance, and that more than 800 observations are needed if information per sire is limited to fewer than 30-40 progeny. A negative environmental correlation between preweaning growth of the female and her subsequent maternal ability has been reported by Mangus and Brinks (1971) and Koch (1972). Such a correlation would be expected to lower the offspring-dam regression estimates of h^2.

The h^2 estimates for yearling weight are given in Table 3. They range between 0.04 and 0.73 in males, between 0.16 and 0.71 in females and between 0.14 and 0.48 across sexes. The corresponding average values are 0.49, 0.48 and 0.41 (Table 5). As these estimates are high, it seems that the trait will respond to selection.

The estimates of h^2 for muscling score and fat depth are given in Table 4. Muscling score h^2 estimates vary very widely from 0.12 to 0.60 in males, from 0.27 to 1.71 in females, from 0.25 to 0.40 in steers, and

from 0.14 to 1.32 across sexes. This wide variation may be partly attributed to the subjective nature of muscling score and to differences in age at measurement in different studies. Unrealistically high estimates of h^2 for muscling score (1.71, 1.32) have been reported by Francoise *et al.* (1973) from the analysis of data on Angus cattle in Hawaii using the paternal half-sib correlation technique.

Average estimates of h^2 for fat depth are 0.24 in males and 0.33 across sexes. The only estimate available for steer data is high (0.57). In general ultrasonic fat depth seems moderately to highly heritable.

2. Genetic parameter estimates due to maternal effects

It has been reported by many workers (Koch and Clark, 1955; Koch, 1972; Thompson, 1976; Willham, 1980; Baker, 1980; Trus and Wilton, 1988; Meyer, 1992) that growth traits in beef cattle are affected by maternal genetic and additive genetic effects, besides other factors. Various workers have estimated and reviewed genetic parameter estimates due to maternal effects on growth traits in beef cattle. The genetic parameter estimates due to maternal effects on birth weight are given in Table 6. The heritability estimates due to additive genetic effects (h^2_A, direct heritability) on birth weight range between 0.14 and 0.61 in different breeds, 0.30 being the average for 43 studies (Table 9). The heritability estimates due to maternal genetic effects (h^2_M, maternal heritability) on birth weight vary from 0.03 to 0.82, the average being 0.10. The correlation between additive genetic and maternal genetic effects (r_{AM}) shows wide variation (from −1.05 to 0.55). The average r_{AM} is large and negative (−0.35), indicating antagonism between the genes for prenatal growth and the genes conditioning the intrauterine environment for heavier weights at birth. Such an antagonism would be a balanced mechanism to maintain birth weight in intermediate ranges (Brown and Galvez, 1969). The maternal environmental variance as a proportion of the phenotypic variance (c^2) averages 0.03 (Table 9). The covariance between the additive genetic and maternal genetic effects as a proportion of the phenotypic variance (c_{AM}) ranges from −0.24 to 0.05. The heritability estimates for the total additive effects (h^2_T, total heritability, after Willham, 1972) on birth weight range from −0.02 to 0.68 in different breeds.

The genetic parameter estimates due to maternal effects on weaning weight are given in Table 7. The average h^2_A, h^2_M and h^2_T are 0.22, 0.13 and 0.23 respectively. The r_{AM} is negative and small (Table 9). The genetic parameter estimates due to maternal effects on yearling weight are presented in Table 8. Values of h^2_A, h^2_M and h^2_T show wide variation (0.12-0.50, 0.02-0.20 and 0.02-0.50 respectively). The r_{AM} value is negative and moderate in magnitude.

The average estimates of genetic parameters due to maternal effects on growth traits are lower than those presented by Baker (1980) from a review of the literature concerning beef traits. For example, the h^2_A, h^2_M, h^2_T and r_{AM} values reported by Baker (1980) are 0.40, 0.19, 0.34 and −0.42 respectively for birth weight and 0.30, 0.52, 0.25 and −0.72 for weaning weight. There is a paucity of information concerning maternal effects on muscling score and fat depth. The only study reported is that of Robinson *et al.* (1992), who analysed data on 9232 Angus, Hereford and Polled Hereford cattle aged between 300 and 600 days at the time of scanning. Average permanent environmental effects of the dam for ultrasonic rump and rib fat were 4% and 11% respectively. Average maternal effects were 6% and 5% respectively.

The literature concerning genetic parameter estimates due to maternal effects on growth traits indicates that there should be little or no loss in genetic progress for the maternal traits when selection is applied to direct and maternal effects, as total heritabilities are at least as high as direct heritabilities. The benefit over reliance on selecting for the direct effect alone could be in the reduction of per cow costs, thereby increasing production efficiency.

Maternal heritabilities were lower than direct heritabilities. This implies that growth traits were determined more by the genetic characteristics of the calf than by those of the dam.

The average correlation between additive genetic and maternal genetic effects is negative for the three growth traits reviewed. It is highest for birth weight (−0.35), followed by yearling weight (−0.26) and weaning weight (−0.15). This estimate of the genetic correlation between additive and maternal effects seems to suggest that many of the same genes possess opposite effects on direct and maternal components of birth, weaning and yearling weights. It indicates a tendency for animals with superior growth genes to have inferior maternal genes and *vice versa* (Garrick, 1990). This would suggest that genes which partition nutrients for growth of the young calf are partly incompatible with genes which partition nutrients for lactation. Garrick (1990) suggests that this negative correlation may be the result of many generations of natural selection with an intermediate optimum. Koch and Clark (1955) are of the view that if r_{AM} is negative more emphasis should be placed on selecting cows on the basis of their calf's weaning weight if selection for maternal ability is to keep pace with selection for growth response. In fact, if extreme emphasis is placed on calf gains alone, particularly on yearling gains, there could actually be a loss in genetic value for milking ability. It must be cautioned that this negative correlation between additive genetic and maternal genetic effects may be induced by environmental factors such as management and husbandry practices.

If r_{AM} is zero, selection for the trait would tend to be more for the genes for growth in the offspring than for maternal influence. If it is positive, selection improves both additive genetic and maternal genetic components. However, if it is negative and high, the optimal procedure would be to select for maternal genetic effects in females and genetic value for growth in males.

A wide variation in the estimates of genetic parameters due to maternal effects on growth traits may be attributed to the method of analysis, as well as other reasons. During the last decade estimates were obtained by comparisons of expected composition of variances and covariances with observed values from different types of relatives. Mainly sire-dam and sire-maternal grandsire models were employed for this purpose. Such comparisons are biased, and are subject to large errors due to the generally small number of relatives involved. Recent estimates have been obtained by the use of animal models with maternal effects, mostly using programs based on software written by Meyer (1991).

3. Repeatability

The repeatability estimates of growth traits are given in Table 10. The repeatability estimates for birth weight (trait of the cow expressed through the calf) range between –0.03 and 0.41 in various breeds, the average values being 0.21 in males, 0.29 in females and 0.23 across sexes (Table 5). A negative estimate for the repeatability of birth weight was reported by Gregory *et al.* (1950) in Hereford cattle. The main reason for this very low estimate might be the small data set used. The average values for repeatability of birth weight (trait of the cow) are lower than the corresponding estimates of heritability for the trait (trait of the calf). It seems that the genotype of the calf is more important than maternal influence in determining birth weight.

The repeatability estimates for weaning weight varied from 0.21 to 0.52 in different breeds. The average values of repeatability for male, female and combined data sets are relatively high, being of the order of 0.44, 0.27 and 0.23 respectively (Table 5). The average repeatability estimates for weaning weight are higher than average heritability estimates for weaning weight. This supports the idea that maternal effects are important in determining the weaning weights of calves. The repeatability estimates for weaning weight are higher than those of birth weight.

The only estimates of the repeatability of yearling weight from the available literature are 0.21 for males and 0.48 for females (Alenda and Martin, 1987). The higher estimate of repeatability of yearling weight in females than in males may be due to the level of feeding in the postweaning period. The male calves were fed *ad libitum*, allowing full expression of individual genetic variability for growth, while the females were restricted to a rate of gain of approximately 0.5 kg per day. Restricted feeding probably created a dependency of postweaning gain on preweaning maternal environment in the females.

Most repeatability estimates have been calculated using the intraclass correlation and the regression of subsequent records on earlier records. Regression repeatabilities are unbiased by any truncation selection that has occurred based on earlier records (Curnow, 1961), whereas the intraclass correlation repeatability of cow productivity considers all records at once; each regression coefficient reflects only the relationship between a specific pair of records of the same cow. A basic assumption for the estimation of repeatability using the regression of later records on earlier calf records of the same cow is that phenotypic variances are homogeneous for both variables.

The degree of adjacency of calf records affects the repeatability estimates. Cunningham and Henderson (1965b) have demonstrated that repeatabilities based on adjacent records tend to be higher than those based on non-adjacent records. It has been shown that repeatability decreases as the degree of adjacency increases. The number of pairs of records in the estimate also decreases, leading to greater variance of the estimator, and it is questionable whether estimates from pairs of records with a degree of adjacency of 5 or above are of much use. This decreasing trend in repeatability estimates has been discussed by Boston *et al.* (1975). The several factors suggested as the possible causes are (1) positively correlated temporary environmental effects among consecutive or closely adjacent records of the same cow (e.g. closely related sires, management and nutrition practices, weather conditions, and effects due to undefinable age of the dam), (2) slight changes in the nature of permanent environmental effects acting on the cow, which could be due to varying rates of physiological ageing (including the time of maturity and of the onset of the decline in production associated with age), or to partial recovery over time from an adverse heifer environment, and (3) progressive selection of the cows.

An estimate of repeatability like h^2 is merely a description of a certain population under certain conditions of the environment. The applicability of the estimate is therefore limited to situations where (1) cattle are reared under conditions similar to those for which the estimate was obtained, and (2) the data are adjusted for the same sources of variation. The repeatability estimates cannot be compared in a straightforward manner. This is because repeatability is due to at least two components and the relationship between them. The cow gives her offspring half her genes. Thus, one-fourth of the genes for growth of the calf are, on average, common to maternal half-sibs. The second component involves the maternal environment created for the calves of the same cow. This involves the expression of genes for the maternal performance of the cow in the trait expressed by her calves, and permanent environmental effects common to calves of the same cow. If a covariance exists between genes for growth and maternal ability, it may be either positive or negative; a negative covariance can mask a positive variance, making comparisons of repeatabilities difficult (Sellers *et al.*, 1970).

4. Phenotypic, genetic and environmental correlations

The phenotypic, genetic and environmental correlations between various performance traits (Tables 11, 12, 13 and 15) have been estimated from different populations, and it is therefore not surprising that differences exist. As these correlations vary between populations, estimates calculated from one environment should be generalised with caution. Environmental correlations are included only if given in the papers cited, but they may be calculated from heritabilities and genetic correlations following the procedures outlined by Falconer (1989).

(a) Growth traits

The phenotypic, genetic and environmental correlations between birth weight and weaning weight are given in Table 11. The phenotypic correlations between the two traits range from 0.11 to 0.94 in various breeds. The average phenotypic correlation is 0.30 in males, 0.39 in females and 0.65 in combined data sets (Table 14). The correlations are positive and moderate to high in magnitude in almost all studies reviewed. These phenotypic correlations between birth weight and weaning weight do not necessarily mean that selecting on one trait will lead to improvement in the other, because a phenotypic correlation is not always a reliable estimate of the genetic relationship existing between the traits; an environmental effect upon two traits could be so strong that a negative genetic correlation is masked.

Estimates of genetic correlation between birth weight and weaning weight range from 0.25±0.34 to 0.99±0.01 in males, from 0.25±0.26 to 0.69 in females and from −0.36±0.22 to 0.83±0.02 across sexes. The negative estimate of genetic correlation between birth weight and weaning weight was reported by Pabst *et al.* (1977) from an analysis of data on Charolais cattle. The small number of observations limits the conclusions which can be drawn from these findings. There are no similar estimates known from the literature except those from Willis *et al.* (1972), who obtained positive correlations between birth weight and weight at 90 days of age with purebred cattle but negative estimates with crosses. Cattle that had been graded up were included in the Charolais data, and this may account for similar results. Most of the genetic correlations between birth weight and weaning weight are high and positive. They seem to indicate that the two traits are under the influence of similar genes, and genetic change in one trait is expected to accompany a change in the other. The environmental correlations between birth and weaning weights are low to moderate.

The phenotypic, genetic and environmental correlations between birth weight and yearling weight are given in Table 12. The average phenotypic correlations between birth weight and yearling weight are positive and almost of similar magnitude (high) in males, females and across sexes (Table 14).

The genetic correlations are also positive and high, ranging from 0.27 to 0.75 in males, 0.41 to 0.60 in females and 0.26 to 0.57 in combined data sets. It may be concluded from these estimates that the same genes tend to influence the two traits, and that selection for one will improve the other as a correlated response, i.e. higher birth weights will generally be associated with higher yearling weights.

The estimates of phenotypic, genetic and environmental correlations between weaning weight and yearling weight are presented in Table 13. The phenotypic correlations between weaning weight and yearling weight vary from 0.57 to 0.85 in different breeds. Most estimates of phenotypic correlations between these two traits are high and positive (averages are 0.76 for males, 0.73 for females and 0.74 for combined sexes.

There is a very wide range in the genetic correlations between weaning weight and yearling weight in different breeds (0.16 to 0.92), with most of the estimates clustered around 0.80. It appears from these positive and high estimates that the two traits are affected by the same genes and that selection for one trait will improve the other. A high and positive genetic correlation seems desirable because selection based on increased weaning weight will automatically improve yearling weight, and will thus result in rapid and economical beef cattle production.

(b) Growth traits, muscling score and fat depth

The phenotypic, genetic and environmental correlations between growth traits and muscling score and fat depth are given in Table 15. The phenotypic and genetic correlations between birth weight and muscling score are generally very low. It seems that there are very few genes that affect both traits and that there will be little correlated change in one trait as a result of selection for the other trait. It can be concluded that a high birth weight may not be a good indicator of muscling at yearling age. The environmental correlations between birth weight and muscling score are also very low, indicating that environments affecting muscling score are independent of those influencing birth weight.

The phenotypic correlations between weaning weight and muscling score are low. The genetic correlations between weaning weight and muscling score vary very widely, from −0.04 to −0.24 in males, from −0.68 to 0.21 in females and from −0.48 to 0.38 in steers.

Reported values are very variable and inconclusive. For example, a genetic correlation of 0.38 between weaning weight and muscling score is high, and it may be said that higher weaning weights may be associated with higher muscling scores at yearling age, while the value of −0.68 seems to indicate the reverse. The subjective nature of muscling score may account for the inconsistent estimates.

Yearling weight has been found to have a moderate phenotypic correlation with muscling score in bulls and steers (0.27), while in females the correlation is low and negative (–0.12). The genetic correlation between yearling weight and muscling score varies from –0.14 to 0.08 in males, from –0.77 to 0.04 in females and from –0.65 to 0.11 across sexes. The environmental correlations between yearling weight and muscling score are positive and high. They indicate that the two traits are affected by almost similar types of environments. This may be expected because an animal that is provided with the environmental conditions to increase muscularity will also put on weight.

The estimates of phenotypic correlation between weaning weight and fat depth range between 0.19 and 0.26 in males while in steers the correlation is –0.13, as reported by Dinkel and Busch (1973) from an analysis of data on grade Hereford steers. The genetic correlation varies from –0.01 to 0.13 in males, while the figure for steers is –1.0. The phenotypic and genetic correlations between yearling weight and fat depth are positive and low to moderate.

Very wide ranges in the estimates of genetic parameters may be attributed to the following factors: (1) the number of observations in the analysis, (2) the method of analysis and estimation, (3) the adjustments for non-genetic factors made on each data set, (4) the genetic constitution of the breeds involved in the studies in different populations, (5) the number of measurements/records (heritability and repeatability estimates may be different for single and multiple records), and (6) sampling variance.

The genetic parameters for various performance traits may be biased for the following reasons: (1) smallness of the data set involved in the analyses, (2) lack of appropriate statistical control over the possible environmental factors, (3) selection, (4) inbreeding, (5) assortative mating, (6) an inappropriate method of estimation, and (7) maternal effects.

Mean values for various genetic parameters (Tables 5, 9 and 14) have been calculated as averages weighted by the number of observations.

IV. Conclusions

The estimates of heritability for growth traits in beef cattle are generally moderate (0.25-0.30). They should, therefore, respond to selection. The estimates of direct heritability are higher than maternal heritabilities for almost all growth traits. Estimates of maternal heritability are highest for weaning weight, followed by yearling and birth weights in turn. This indicates that maternal effects may be more important for weaning weight than for birth or yearling weight. This is further supported by the fact that the average repeatability estimate for weaning weight (trait of the dam) is higher than the average heritability for the trait (trait of the calf). Estimates of direct heritability for growth traits are moderate, while corresponding maternal heritability estimates range between low and the low side of moderate. The estimates of direct and total heritability are almost of similar magnitude for the three growth traits. Any of these traits can be expected to respond to selection, even though the genetic correlation between additive and maternal effects is negative. However, the rate of response will not be as high as expected if r_{AM} is zero. This negative correlation suggests that many of the genes which favour the milking and mothering ability of the cow are partly detrimental for growth of the young calf.

Ultrasonic fat depth and visual muscling score are moderately to highly heritable.

The repeatability estimates of birth weight are lower than those for weaning weight, while that of yearling weight is low to moderate. The moderate repeatability of weaning weight indicates that selection on the basis of the first record may be effective in improving the overall performance of the herd in the next year. It can be concluded that cows tend to repeat their previous performance to a higher degree for weaning weight of their calves than for birth weight.

The average genetic correlations between growth traits are generally high (0.41-0.88), suggesting that many of the same genes affect body weights at different ages. The positive and high genetic correlations between birth weight and body weights at later ages seem to be undesirable, because this will increase the incidence of dystocia. Therefore, it may be imperative to monitor birth weight when selecting for higher weaning and yearling weights.

Growth traits do not seem to be highly genetically correlated with visual muscling score and fat depth. The genetic correlation between muscling score and fat depth is moderate and negative; it seems that higher muscling scores are generally associated with decreased fat depth.

There is a clear need for more thorough studies with large data sets using more sophisticated techniques of data analysis, such as multivariate restricted maximum likelihood, particularly for the computation of genetic parameter estimates due to maternal effects on postweaning performance traits (yearling weight, muscling score and ultrasonic fat depth). Very few studies have been found in the literature regarding genetic and phenotypic relationships between growth traits and muscling score and ultrasonic fat depth. This suggests another area of future research that may be vital for efficient and economical beef production, namely the nature of the relationship between growth traits and ultrasonic fat depth. There is also a serious deficiency in the current state of knowledge on the genetic relationships between various performance traits, as maternal effects may be a source of bias. Further investigations involving phenotypic and genetic analysis of the correlations between various performance traits, including maternal effects in the model for analysis, may therefore be warranted.

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V. References

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Table 1. Heritability estimates for birth weight

Breed	Country	Method	Estimate			Reference
			Males	Females	Combined	
HEF	USA	rPHS	0.53 (880)	–	–	1
HEF	USA	rPHS	–	–	0.45 (281)	2
HEF	USA	rPHS	–	–	1.00 (74)	2
HEF	USA	rPHS	0.72 (635)	–	–	3
HEF	USA	rPHS	0.67 (414)	–	–	4
HEF	USA	rPHS	–	0.22±0.10 (793)	–	5
HEF	USA	rPHS	0.54 (616)	–	–	6
HEF	USA	rPHS	–	–	0.57±0.19 (789)	7
HEF	USA	bOD	–	–	0.32±0.10	7
HEF	USA	rPHS	0.49±0.09 (1769)	0.57±0.12 (1693)	–	8
HEF	UK	rPHS	–	–	0.23±0.05 (2650)	9
HEF	USA	rPHS	–	0.55 (377)	–	10
HEF	USA	bOM	–	0.46 (377)	–	10
HEF	USA	rPHS	0.54±0.10 (1379)	–	–	11
HEF	USA	rPHS	0.34±0.03	0.36±0.03	–	12
HEF	Canada	rPHS	0.35 (764)	–	–	13
HEF	USA	rPHS	–	–	0.41 (14436)	14
HEF	USA	rPHS	–	–	0.28 (4423)	15
HEF	USA	rFS	–	–	0.45 (976)	15
HEF	USA	bOD	–	–	0.45	15
HEF	USA	bOS	–	–	0.21	15
ANG	USA	rPHS	–	–	0.31±0.27 (932)	7
ANG	USA	bOD	–	–	0.22±0.08	7
ANG	USA	rPHS	0.49±0.10 (1101)	0.36±0.10 (1012)	0.40±0.07 (2113)	11
ANG	USA	REMLS	0.70 (717)	–	–	16
ANG	USA	rPHS	–	–	0.19 (26 426)	14
ANG	USA	rPHS	0.51±0.09	0.41±0.09	–	17
RANG	USA	rPHS	–	–	0.46±0.02 (41 184)	18
SIM	USA	rPHS	–	–	0.32±0.04 (5578)	19
SIM	USA	rPHS	0.42±0.05	0.30±0.03	0.31±0.02 (17 297)	20
SIM	Canada	rPHS	–	–	0.19 (4345)	21
CHA	Cuba	rPHS	–	–	0.25±0.6 (212)	22
CHA	France	rPHS	0.32±0.12 (647)	–	–	23
CHA	Canada	REMLS	–	–	0.25 (1419)	24
SGT	Cuba	rPHS	–	–	0.39±0.3 (435)	22
SGT	USA	rPHS	0.38±0.12 (939)	0.24±0.10 (955)	0.32±0.07 (1894)	25
LIM	USA	rPHS	0.19±0.04	0.17±0.02	0.16±0.02 (197 000)	26
BSHH	Canada	bOD/S	–	–	0.21±0.10 (892)	27
BSHH	Canada	rPHS	0.17±0.18 (327)	–	–	28
BSHH	Canada	bSS	0.30±0.13	–	–	28
SDV	Nigeria	rPHS	–	–	0.26±0.01 (23 708)	29
Zebu	Nigeria	rPHS	–	–	0.28±0.01 (31 488)	29
HEF, ANG & RANG	USA	rPHS	0.43±0.07	0.35±0.06	–	30
HEF, ANG & BSxZ	USA	rPHS	–	0.27±0.07 (779)	–	31
HxZ	Cuba	rPHS	–	–	0.62±0.40 (1160)	22
CHA, BA & LIM	Cuba	rPHS	–	–	0.09±0.10 (4955)	22
ANG & SHH	France	rPHS	0.31±0.06 (2673)	–	–	23
HEF & GHEF	USA	rPHS	–	0.30±0.12 (647)	–	32
SBP	USA	rPHS	–	0.37±0.07 (2092)	–	32
SBP1	Canada	rPHS	0.47 (1313)	–	–	13
Xbred	Canada	rPHS	–	0.60±0.16 (505)	–	33
ZX	Australia	REMLS	–	–	0.52±0.13 (1188)	34
ZX	Australia	REMLA	–	–	0.78 (1267)	35
	Australia	REMLS	–	–	0.57 (1505)	36

Breeds: HEF, Hereford; ANG, Angus; RANG, Red Angus; SIM, Simmental; CHA, Charolais; SGT, Santa Gertrudis; LIM, Limousin; BSHH, Beef Shorthorn; SDV, South Devon; BSxZ, Brown Swiss cross zebu; HxZ, Holstein cross zebu; BA, Blonde d'Aquitaine; SHH, Shorthorn; GHEF, Grade Hereford; SBP, a synthetic beef cattle population with 35.7% Angus,

34.7% Charolais, 21.7% Galloway, 4.5% Brown Swiss and 3.4% others (in 1978); SBP1, a synthetic beef cattle population with approximately 33% Charolais, 33% Angus and 20% Galloway breeding with small contributions from other beef breeds; Xbred, crossbred consisting of 1/2 or 3/4 Brahman and 1/2, 3/4, 7/8 or 15/16 Sahiwal crosses with Beef Shorthorn; ZX, zebu cross.

Methods: rPHS, correlation between paternal half-sibs; bOD, regression of offspring on dam; bOM, regression of offspring on mid-parent cumulative selection differential; rFS, correlation between full-sibs; bOS, regression of offspring on sire; REMLS, restricted maximum likelihood (sire model); bOD/S, intrasire regression of offspring on dam; bSS, regression of son on sire; REMLA, restricted maximum likelihood (multivariate animal model).

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Figures in parentheses indicate number of observations.

Table 2. Heritability estimates for weaning weight

Breed	Country	Method	Estimate			Reference
			Males	Females	Combined	
HEF	USA	rPHS	0.28 *(880)	–	–	1
HEF	USA	rPHS	–	–	0.26 (270)	2
HEF	USA	rPHS	–	–	0.52 (69)	2
HEF	USA	rPHS	0.23 *(635)	–	–	3
HEF	USA	rPHS	0.28±0.32 (329)	0.57±0.41 (332)	–	4
HEF	USA	rPHS	0.11 (414)	–	–	5
HEF	USA	rPHS	–	0.25±0.11 (748)	–	6
HEF	USA	rPHS	0.08 *(499)	0.31 (420)	0.17 (919)	7
HEF	USA	rPHS	0.24 *(616)	–	–	8
HEF	USA	rPHS	0.33±0.08 (1915)	–	–	9
HEF	USA	rPHS	–	–	0.43 (1648)	10
HEF	USA	rPHS	0.15±0.07 (1769)	0.25±0.10 (1693)	–	11
HEF	UK	rPHS	–	–	0.38±0.06 (4439)	12
HEF	USA	rPHS	–	0.18 (377)	–	13
HEF	USA	bOM	–	0.12 (377)	–	13
HEF	USA	rPHS	0.43±0.09 (1379)	–	–	14
HEF	Canada	ML	0.18	0.24	–	15
HEF	USA	rPHS	0.23±0.02	0.18±0.01	–	16
HEF	USA	rPHS	0.15±0.17 (578)	–	–	17
HEF	Canada	rPHS	0.14 (764)	–	–	18
HEF	USA	rPHS	–	–	0.13 (46 618)	19
HEF	USA	rPHS	–	–	0.28 (4423)	20
HEF	USA	rFS	–	–	0.88 (976)	20
HEF	USA	bOD	–	–	0.28	20
HEF	USA	bOS	–	–	0.06	20
HEF	USA	REMLS	0.12±0.12 (824)	–	–	21
ANG	USA	rPHS	0.32±0.16 (436)	–	–	9
ANG	USA	rPHS	–	–	0.47 (3190)	10
ANG	USA	rPHS	0.37±0.09 (1101)	0.21±0.08 (1012)	0.35±0.06 (2113)	14
ANG	Canada	ML	0.30	0.40	–	15
ANG	USA	REMLS	0.46±0.05 (717)	–	–	22
ANG	USA	rPHS	–	–	0.16 (35 227)	19
ANG	USA	rPHS	0.30±0.08	0.21±0.07	–	23
AANG	UK	rPHS	–	–	0.39±0.10 (1482)	12
RANG	USA	rPHS	–	–	0.39±0.02 (41 184)	24
SIM	USA	rPHS	–	–	0.28±0.04 (5578)	25
SIM	USA	rPHS	0.24±0.05	0.21±0.03	0.22±0.02 (17 297)	26
SIM	Canada	ML	0.31	0.40	–	15
CHA	Canada	ML	0.23	0.30	–	15
CHA	France	rPHS	0.18±0.09 (699)	–	–	27
CHA	Canada	REMLS	–	–	0.09 (1419)	28
SGT	USA	rPHS	0.30±0.11 (939)	0.45±0.12 (955)	0.42±0.08 (1894)	29
LIM	Canada	ML	0.12	0.15	–	15
LIM	USA	rPHS	0.06±0.02	0.09±0.02	0.08±0.01 (197000)	30
SSH	Canada	ML	0.26	0.33	–	15
BSHH	Canada	bOD/S	–	–	0.13±0.11 (892)	31
BSHH	Canada	rPHS	0.47±0.20 (327)	–	–	32
BSHH	Canada	bSS	0.34±0.22	–	–	32
DEV	UK	rPHS	–	–	0.47±0.10 (1736)	12
SDV	Nigeria	rPHS	–	–	0.21±0.01 (23708)	33
SSX	UK	rPHS	–	–	0.29±0.05 (1640)	12
GHEF	USA	rPHS	0.09 *(313)	–	–	34
GHEF	USA	bOD	0.84±0.23 *(151)	–	–	34
GHEF	USA	rPHS	0.54 *(256)	–	–	34
~~GHEF~~	~~USA~~	~~bOD~~	~~-0.13±0.24 *(120)~~	~~–~~	~~–~~	~~34~~
GHEF	USA	rPHS	0.40 (679)	–	–	35
Zebu	Nigeria	rPHS	–	–	0.31±0.01 (31 488)	33
BRH	Australia	REMLS	–	–	0.35±0.11 (2052)	36
BRH	Australia	REMLS	–	–	0.64±0.18 (1166)	36
Xbred	Australia	REMLS	–	–	0.33±0.11 (1188)	36
ZX	Australia	REMLA	–	–	0.56 (1267)	37
ZX	Australia	REMLS	–	–	0.21 (1505)	38
HEF, ANG & RANG	USA	rPHS	0.63±0.08	0.69±0.10	–	39

HEF, ANG & RANG	USA	rPHS	–	0.14±0.06 (779)	–	40
BA, CHA & LIM	France	rPHS	0.21±0.05 (3098)	–	–	27
ANG & SHH	USA	rPHS	–	0.00±0.06 (647)	–	41
HEF & GHEF	USA	rPHS	–	0.20±0.06 (2092)	–	41
HEF & AANG	Canada	rPHS	–	–	0.32 (84 021)	42
SBP	Canada	rPHS	0.25 (1313)	–	–	18
SBP1	Canada	rPHS	–	0.20±0.13 (505)	–	43

Breeds: HEF, Hereford; ANG, Angus; AANG, Aberdeen-Angus; RANG, Red Angus; SIM, Simmental; CHA, Charolais; SGT, Santa Gertrudis; LIM, Limousin; SHH, Shorthorn; BSHH, Beef Shorthorn; DEV, Devon; SDV, South Devon; SSX, Sussex; GHEF, Grade Hereford; BRH, Brahman; Xbred, crossbred; ZX, zebu cross; BA, Blonde d'Aquitaine; SBP, synthetic beef cattle population with 35.7% Angus, 34.7% Charolais, 21.7% Galloway, 4.5% Brown Swiss & 3.4% others (in 1978); SBP1, synthetic beef cattle population with approximately 33% Charolais, 33% Angus and 20% Galloway breeding with small contributions from other beef breeds.

Methods: rPHS, correlation between paternal half-sibs; bOM, regression of offspring on mid-parent cumulative selection differential; ML, multitrait maximum likelihood; rFS, correlation between full-sibs; bOD, regression of offspring on dam; bOS, regression of offspring on sire; REMLS, restricted maximum likelihood (sire model); bOD/S, intrasire regression of offspring on dam; bSS, regression of son on sire; REMLA, restricted maximum likelihood (multivariate animal model).

References: 1, Knapp and Clark (1950); 2, Gregory et al. (1950); 3, Shelby et al. (1955); 4, Pahnish et al. (1961); 5, Lasley et al. (1961); 6, Swiger (1961); 7, Blackwell et al. (1962); 8, Shelby et al. (1963); 9, Minyard and Dinkel (1965); 10, Cunningham and Henderson (1965a); 11, Koch et al. (1973); 12, Pabst et al. (1977); 13, Koch (1978); 14, Nelsen and Kress (1979); 15, Schaeffer and Wilton (1981); 16, Buchanan et al. (1982); 17, Neely et al. (1982); 18, Sharma et al. (1985); 19, Wilson et al. (1986); 20, Cantet et al. (1988); 21, Lamb et al. (1990); 22, Knights et al. (1984); 23, Alenda and Martin (1987); 24, Winder et al. (1990); 25, Burfening et al. (1978a); 26, Burfening et al. (1978b); 27, Renand (1985); 28, Johnston et al. (1992a); 29, Aaron et al. (1987); 30, Massey and Benyshek (1981); 31, Fahmy and Lalande (1973); 32, Anderson et al. (1974); 33, Iloeje (1986); 34, Rollins and Wagnon (1956); 35, Dinkel and Busch (1973); 36, Robinson and Rourke (1992); 37, Mackinnon et al. (1991); 38, Mackinnon and Meyer (1992); 39, Bourdon and Brinks (1982); 40, Smith et al. (1989); 41, Swiger et al. (1962); 42, Kennedy and Henderson (1975a); 43, Arthur and Makarechian (1992).

Figures in parentheses indicate number of observations.

* Steers.

Table 3. Heritability estimates for yearling weight

Breed	Country	Method	Estimate			Reference
			Males	Females	Combined	
HEF	USA	rPHS	0.10 *(499)	0.71 (420)	0.34 (919)	1
HEF	UK	rPHS	–	–	0.27±0.07 (1760)	2
HEF	USA	rPHS	–	0.33 (377)	–	3
HEF	USA	bOM	–	0.43 (377)	–	3
HEF	USA	rPHS	0.49±0.28 (695)	–	–	4
HEF	Canada	ML	0.18	0.36	–	5
HEF	USA	rPHS	0.23±0.02	0.37±0.03	–	6
HEF	USA	rPHS	0.33±0.19 (578)	–	–	7
HEF	Canada	rPHS	0.24 (414)	–	–	8
HEF	New Zealand	REMLS	–	–	0.17±0.06 (2414)	9
ANG	Canada	ML	0.21	0.52	–	5
ANG	USA	REMLS	0.49±0.05 (717)	–	–	10
ANG	USA	rPHS	0.36±0.08	0.18±0.07	–	11
RANG	USA	rPHS	–	–	0.40±0.02 (41 184)	12
SIM	Canada	ML	0.19	0.44	–	5
CHA	Canada	ML	0.19	0.44	–	5
CHA	France	rPHS	0.32±0.12 (699)	–	–	13
CHA	Canada	REMLS	–	–	0.16 (1418)	14
LIM	USA	rPHS	0.13±0.05	0.16±0.03	0.14±0.02	15
LIM	Canada	ML	0.08	0.26	–	5
SHH	Canada	ML	0.15	0.36	–	5
BSHH	Canada	rPHS	0.04±0.16 (327)	–	–	16
BSHH	Canada	bSS	0.47±0.23	–	–	16
SDV	Nigeria	rPHS	–	–	0.33±0.01 (23 708)	17
Zebu	Nigeria	rPHS	–	–	0.37±0.01 (31 488)	17
BRH	Australia	REMLS	–	–	0.30±0.11 (1052)	18
Xbred	Australia	REMLS	–	–	0.18±0.08 (1170)	18
HEF & AANG	Canada	rPHS	–	–	0.48 (84 021)	19
HEF, ANG & RANG	USA	rPHS	0.73±0.11	0.66±0.10	–	20
HEF, ANG & RANG	USA	rPHS	–	0.29±0.08 (779)	–	21
SBP	Canada	rPHS	0.41 (660)	–	–	8
SBP1	Canada	rPHS	–	0.44±0.15 (505)	–	22
ZX	Australia	REMLA	–	–	0.48 (1267)	23
ZX	Australia	REMLS	–	–	0.29 (1505)	24

Breeds: HEF, Hereford; ANG, Angus; RANG, Red Angus; SIM, Simmental; CHA, Charolais; LIM, Limousin, SHH, Shorthorn; BSHH, Beef Shorthorn; SDV, South Devon; BRH, Brahman; Xbred, crossbred consisting of 1/2 or 3/4 Brahman and 1/2, 3/4, 7/8 or 15/16 Sahiwal crosses with Beef Shorthorn; AANG, Aberdeen-Angus; SBP, synthetic beef cattle population with 35.7% Angus, 34.7% Charolais, 21.7% Galloway, 4.5% Brown Swiss, 3.4% others (in 1978); SBP1, a synthetic beef cattle population with approximately 33% Charolais, 33% Angus and 20% Galloway breeding with small contributions from other beef breeds; ZX, zebu cross.

Methods: rPHS, correlation between paternal half-sibs; bOM, regression of offspring on mid-parent cumulative selection differential; ML, multiple trait maximum likelihood; REMLS, restricted maximum likelihood (sire model); bSS, regression of son on sire; REMLA, restricted maximum likelihood (multivariate animal model)

References: 1, Blackwell et al. (1962); 2, Pabst et al. (1977); 3, Koch (1978); 4, Mavrogenis et al. (1978); 5, Schaeffer and Wilton (1981); 6, Buchanan et al. (1982); 7, Neely et al. (1982); 8, Sharma et al. (1985); 9, Morris et al. (1992); 10, Knights et al. (1984); 11, Alenda and Martin (1987); 12, Winder et al. (1990); 13, Renand and Gaillard (1982); 14, Johnston et al. (1992); 15, Massey and Benyshek (1981); 16, Anderson et al. (1974); 17, Iloeje (1986); 18, Robinson and Rourke (1992); 19, Kennedy and Henderson (1975a); 20, Bourdon and Brinks (1982); 21, Smith et al. (1989); 22, Arthur and Makarechian (1992); 23, Mackinnon et al. (1991); 24, Mackinnon and Meyer (1992)

Figures in parentheses indicate number of observations.

* Steers.

Table 4. Heritability estimates for ultrasonic fat depth and muscling score

Breed	Country	Method	Estimate			Reference
			Males	Females	Combined	
Ultrasonic fat depth						
HEF	USA	rPHS	0.21±0.23 (695)	–	–	1
HEF	USA	rPHS	0.28±0.18 (578)	–	–	2
HEF	USA	REMLS	0.24±0.14 (824)	–	–	3
HEF	USA	REMLS	–	–	0.26 (3482)	4
HEF	Australia	REMLA	–	–	0.46 (1960)	5
HEF	Australia	REMLA	–	–	0.22 (1497)	5
PHEF	Australia	REMLA	–	–	0.20 (2047)	5
GHEF	USA	rPHS	0.57 *(679)	–	–	6
ANG	Australia	REMLA	–	–	0.42 (1910)	5
ANG	Australia	REMLA	–	–	0.41 (1818)	5
HEF, ANG & PHEF	Australia	REMLA	–	–	0.34 (9232)	5
Muscling score						
HEF	USA	rPHS	0.40 *(499)	0.34 (420)	–	7
HEF	Hawaii	rPHS	0.12±0.15	0.57±0.16	0.41±0.11	8
HEF	USA	rPHS	–	0.27 (377)	–	9
HEF	USA	rPHS	0.24±0.02	0.30±0.03	–	10
HEF	Australia	REMLA	–	–	0.14 (1960)	5
GHEF	USA	rPHS	0.25 *(679)	–	–	6
ANG	Hawaii	rPHS	0.61±0.53	1.71±0.83	1.32±0.50	8
ANG	Australia	REMLA	–	–	0.17 (1910)	5
CHA	France	rPHS	0.21±0.10 (699)	–	–	11
CHA, BA & LIM	France	rPHS	0.28±0.05 (3098)	–	–	11
HEF & ANG	Hawaii	rPHS	–	–	0.56±0.11 (1759)	8

Breeds: HEF, Hereford; PHEF, Polled Hereford; GHEF, Grade Hereford; ANG, Angus; CHA, Charolais ; BA, Blonde d'Aquitaine; LIM, Limousin.

Methods: rPHS, correlation between paternal half-sibs ; REMLS, restricted maximum likelihood (sire model); REMLA, restricted maximum likelihood (animal model).

References: 1, Mavrogenis et al. (1978); 2, Neely et al. (1982); 3, Lamb et al. (1990); 4, Arnold et al. (1991); 5, Robinson et al. (1992); 6, Dinkel and Busch (1973); 7, Blackwell et al. (1962); 8, Francoise et al. (1973); 9, Koch (1978); 10, Buchanan et al. (1982); 11, Renand (1985).

Figures in parentheses indicate number of observations.

* Steers.

Table 5. Average heritability and repeatability estimates for various performance traits

Sexes		Birth weight	Weaning weight	Yearling weight	Muscling score	Fat depth
Heritability estimates (for traits of calf)						
Males	No.[a]	14	16	9	2	3
	Average	0.46	0.26	0.49	0.24	0.24
	Range	0.17-0.72	0.06-0.63	0.04-0.73	0.12-0.60	0.21-0.28
Females	No.	10	12	7	2	–
	Average	0.39	0.23	0.48	0.31	–
	Range	0.17-0.60	0.00-0.69	0.16-0.71	0.27-1.71	–
Steers	No.	–	9	1	2	1
	Average	–	0.27	0.10	0.31	0.57
	Range	–	–0.13-0.84	–	0.25-0.40	–
Combined	No.	27	29	12	3	7
	Average	0.24	0.20	0.41	0.28	0.33
	Range	0.09-1.00	0.06-0.88	0.14-0.48	0.14-1.32	0.20-0.46
Repeatability estimates (for traits of dam)						
Males	No.	3	8	1	–	–
	Average	0.21	0.44	0.21	–	–
	Range	0.14-0.26	0.42-0.52	–	–	–
Females	No.	1	5	1	–	–
	Average	0.29	0.27	0.48	–	–
	Range	–	0.25-0.50	–	–	–
Steers	No.	–	4	–	–	–
	Average	–	0.24	–	–	–
	Range	–	0.19-0.51	–	–	–
Combined	No.	5	10	–	–	–
	Average	0.23	0.23	–	–	–
	Range	–0.03-0.41	0.21-0.52	–	–	–

[a] No. of studies.

Table 6. Genetic parameter estimates due to maternal effects on birth weight

Breed	Country	No.	Model	Estimate						Reference
				h^2_A	h^2_M	r_{AM}	c^2	c_{AM}	h^2_T	
HEF	USA	789	–	0.56	0.30	–0.58	–	–0.24	0.36	1
HEF	USA	1012[a]		0.36	0.82	–0.51	–	–	0.35	2
HEF	USA	4423	–	0.18	0.21	–1.05	–	–0.21	–0.02	3
HEF	Canada	175 282	SMGS	0.39	0.13	–0.39	–	–	0.32	4
HEF	USA	–	AMMP	0.43	0.12	0.07	0.02	0.02	0.51	5
HEF	USA	2039	SDSMGS	0.58	0.22	–0.13	0.03	–0.05	0.62	6
HEF	Australia	5488	AM	0.56	–	–	–	–	0.56	7
HEF	Australia	5488	AMP	0.49	–	–	0.10	–	0.49	7
HEF	Australia	5488	AMM	0.39	0.14	–	–	–	0.46	7
HEF	Australia	5488	AMM1	0.38	0.14	0.05	–	0.01	0.47	7
HEF	Australia	5488	AMMP1	0.42	0.09	–	0.05	–	0.46	7
HEF	Australia	5488	AMMP	0.41	0.08	0.04	0.05	0.01	0.46	7
HEF	USA	2039	SDSMGS	0.58	0.22	–0.13	0.03	–0.05	0.62	8
PHEF	Australia	3414	*AMMP1	0.43	0.10	–	0.09	–	0.48	9
ANG	USA	932	–	0.14	0.25	–0.39	–	–0.07	0.17	1
ANG	Canada	50767	SMGS	0.37	0.13	–0.34	–	–	0.32	4
ANG	USA	2514	SDSMGS	0.42	0.22	–0.12	–0.38	–0.04	0.47	6
ANG	Australia	4036	AM	0.52	–	–	–	–	0.52	7
ANG	Australia	4036	AMP	0.47	–	–	0.08	–	0.47	7
ANG	Australia	4036	AMM	0.40	0.13	–	–	–	0.46	7
ANG	Australia	4036	AMM1	0.34	0.10	0.27	–	0.05	0.47	7
ANG	Australia	4036	AMMP1	0.42	0.08	–	0.04	–	0.46	7
ANG	Australia	4036	AMMP	0.36	0.07	0.29	0.03	0.05	0.46	7
ANG	USA	2514	SDSMGS	0.42	0.22	–0.12	–0.38	–0.04	0.47	8
ANG	Australia	4036	*AMMP1	0.44	0.08	–	0.03	–	0.48	10
SIM	USA	4196	–	0.21	0.11	–0.24	–	–	0.21	11
SIM	USA	497 409	–	0.16	0.06	–0.44	–	–	0.13	12
SIM	Canada	60 807	SMGS	0.34	0.20	–0.22	–	–	0.36	4
SIM	USA	296 659	SMGS	0.44	0.12	–0.38	–	–0.09	0.37	13
SIM	Australia	58 618	AMM1	0.33	0.07	–0.04	–	–0.01	0.36	14
SHH	Canada	15 839	SMGS	0.27	0.20	0.55	–	–	0.56	4
CHA	Canada	31 252	SMGS	0.42	0.17	–0.39	–	–	0.35	4
LIM	USA	78 088	SDSMGS	0.22	0.05	–0.16	0.05	–0.02	0.22	15
BRG	USA	20 750	SDSMGS	0.25	0.13	–0.12	0.00	–0.02	0.28	15
BRG	USA	32 215	MTPEA	0.28	0.12	–0.52	–	–	0.20	16
SGT	USA	10 768	MTPEA	0.34	0.26	–0.58	–	–	0.21	16
BM	USA	2388	MTPEA	0.22	0.55	–0.53	–	–	0.22	16
BRH	USA	5459	MTPEA	0.37	0.18	–0.15	–	–	0.40	16
AX	Australia	1406	SDSMGS	0.47	0.05	–	0.07	–	0.49	17
HSX	Australia	1346	SDSMGS	0.23	0.03	–	0.18	–	0.24	17
BRHX	Australia	1081	SDSMGS	0.45	0.14	–	0.00	–	0.52	17
ZX	Australia	1267	AMM1	0.61	0.11	0.01	–	0.02	0.68	18
Xbred	Australia	1188	AM	0.58	–	–	–	–	0.58	19
Xbred	Australia	1188	AMM	0.45	0.10	–	–	–	0.55	19
WOKA	Australia	3769	*AMMP1	0.52	0.06	–	0.04	–	0.55	9

Breeds: HEF, Hereford; PHEF, Polled Hereford; ANG, Angus; SIM, Simmental; SHH, Shorthorn; CHA, Charolais; LIM, Limousin; BRG, Brangus; SGT, Santa Gertrudis; BM, Beefmaster; BRH, Brahman; AX, Africander cross; HSX, Hereford Shorthorn cross; BRHX, Brahman cross; ZX, Zebu cross; Xbred, crossbred consisting of 1/2, 3/4 Brahman and 1/2, 3/4, 7/8 or 15/16 Sahiwal with Beef Shorthorn; WOKA, Wokalup, a synthetic breed formed by mating Charolais X Brahman bulls with Friesian X Angus or Hereford cows.

Models: SMGS, sire-maternal grandsire model; AMMP, animal model with permanent environmental dam effect and maternal genetic effect and $\sigma_{AM} \neq 0$; SDSMGS, sire-dam model and sire-maternal grandsire model; AM, simple animal model; AMP, animal model with permanent environmental dam effect; AMM, animal model with maternal genetic effect and $\sigma_{AM}=0$; AMM1, animal model with maternal genetic effect and $\sigma_{AM} \neq 0$; AMMP1, animal model with permanent environmental dam effect and maternal genetic effect and $\sigma_{AM}=0$; MTPEA, multiple-trait pseudo expectation approach.

* Bivariate.

References: 1, Brown and Galvez (1969); 2, Nelsen et al. (1984); 3, Cantet et al. (1988); 4, Trus and Wilton (1988); 5, Koch (1989) cited by Meyer (1992); 6, Brown et al. (1990); 7, Meyer (1992); 8, Johnson et al. (1992); 9, Meyer et al. (1992a); 10, Meyer et al. (1992b); 11, Burfening et al. (1981); 12, Quaas et al. (1985); 13, Garrick et al. (1989); 14, Swalve (1992); 15, Bertrand and Benyshek (1987); 16, Kriese et al. (1991); 17, Hetzel et al. (1990); 18, Mackinnon et al. (1991); 19, Robinson and Rourke (1992).

Symbols used: h^2_A = direct heritability (heritability of the additive genetic effects); h^2_M, maternal heritability (heritability of the maternal genetic effects); r_{AM}, direct-maternal genetic correlation i.e. correlation between additive genetic and maternal genetic effects; c^2, maternal environmental variance as a proportion of the phenotypic variance; c_{AM}, direct-maternal genetic covariance as a proportion of the phenotypic variance; h^2_T, heritability for the total additive effects as proposed by Willham (1972).

Table 7. Genetic parameter estimates due to maternal effects on weaning weight

Breed	Country	No.	Model	Estimate						Reference
				h^2_A	h^2_M	r_{AM}	c^2	c_{AM}	h^2_T	
HEF	USA	–	–	0.18	0.24	0.25	–	–	0.38	1
HEF	USA	4423	–	0.32	0.27	–0.57	–	–0.17	0.20	2
HEF	USA	–	AMMP	0.16	0.19	–0.20	0.26	–0.03	0.20	3
HEF	USA	1835	SDSMGS	0.66	0.43	–0.08	–0.22	–0.04	0.81	4
HEF	Australia	7003	AM	0.26	–	–	–	–	0.26	5
HEF	Australia	7003	AMP	0.10	–	–	0.29	–	0.10	5
HEF	Australia	7003	AMM	0.07	0.34	–	–	–	0.24	5
HEF	Australia	7003	AMM1	0.14	0.46	–0.59	–	–0.15	0.14	5
HEF	Australia	7003	AMMP1	0.09	0.07	–	0.24	–	0.12	5
HEF	Australia	7003	AMMP	0.14	0.13	–0.59	0.23	–0.08	0.09	5
HEF	USA	1835	SDSMGS	0.66	0.43	–0.08	–0.22	–0.04	0.81	6
HEF	USA	–	SDSMGS	0.24	0.24	–0.28	0.08	–0.06	0.25	7
PHEF	USA	–	SDSMGS	0.23	0.30	–0.27	0.03	–0.07	0.26	7
PHEF	Australia	3088	*AMMP1	0.19	0.13	–	0.20	–	0.26	8
CHEF	USA	–	SDSMGS	0.22	0.33	–0.26	0.03	–0.07	0.28	7
ANG	USA	–	–	0.24	0.18	0.15	–	–	0.38	1
ANG	USA	2309	SDSMGS	0.63	0.16	–0.36	-0.31	–0.11	0.54	4
ANG	Australia	3465	AM	0.44	–	–	–	–	0.44	5
ANG	Australia	3465	AMP	0.32	–	–	0.13	–	0.32	5
ANG	Australia	3465	AMM	0.22	0.20	–	–	–	0.32	5
ANG	Australia	3465	AMM1	0.19	0.18	0.20	–	0.04	0.33	5
ANG	Australia	3465	AMMP1	0.23	0.16	–	0.04	–	0.31	5
ANG	Australia	3465	AMMP	0.20	0.14	0.22	0.04	0.04	0.32	5
ANG	USA	2309	SDSMGS	0.63	0.16	–0.36	–0.31	–0.11	0.54	6
ANG	Australia	3465	*AMMP1	0.26	0.11	–	0.05	–	0.32	9
RANG	USA	41 184	SMGS	0.40	0.10	–	–	–	0.45	10
SIM	USA	768 419	SMGS	0.12	0.08	–0.04	–	–	0.15	11
SIM	Australia	15 605	SMGS	0.10	0.13	0.04	–	0.01	0.17	12
SIM	USA	114 899	SMGS	0.12	0.09	0.16	0.07	0.02	0.19	13
SIM	USA	425 085	SMGS	0.36	0.19	–0.32	–	–0.08	0.33	14
SIM	UK	8206	AM	0.30	–	–	–	–	0.30	15
SIM	UK	8897	AM	0.32	–	–	–	–	0.32	16
SIM	UK	8897	AMP	0.19	–	–	0.08	–	0.19	16
SIM	UK	8897	AMM	0.19	0.07	–	–	–	0.23	16
SIM	Australia	52 097	AMMP	0.35	0.18	–0.39	0.08	–0.10	0.29	17
SGT	USA	23 180	MTPEA	0.25	0.18	–0.43	–	–	0.20	18
LIM	USA	53 494	SDSMGS	0.16	0.15	–0.30	0.06	–0.05	0.17	19
BRG	USA	46 661	SDSMGS	0.28	0.20	–0.29	0.04	–0.07	0.28	19
BRG	USA	58 932	MTPEA	0.21	0.15	–0.23	–	–	0.22	18
BRG	USA	7211	MTPEA	0.21	0.21	–0.06	–	–	0.30	18
SNP	USA	4634	SDSMGS	0.21	0.47	–0.57	–0.39	–0.18	0.18	20
BRH	USA	12 559	MTPEA	0.23	0.16	0.15	–	–	0.60	18
BRH	Australia	2052	AM	0.37	–	–	–	–	0.37	21
BRH	Australia	1166	AMM	0.52	0.07	–	–	–	0.56	21
BRH	Australia	2052	AMM	0.35	0.04	–	–	–	0.37	21
BRH	Australia	1166	AM	0.64	–	–	–	–	0.64	21
NLR	Brasil	7415	–	0.26	0.28	–0.91	–	–	0.02	22
Xbred	Australia	1188	AM	0.58	–	–	–	–	0.58	21
Xbred	Australia	1188	AMM	0.31	0.19	–	–	–	0.41	21
AX	Australia	–	SDSMGS	0.15	0.30	–	0.06	–	0.30	23
HSX	Australia	–	SDSMGS	0.20	0.12	–	0.19	–	0.25	23
BRHX	Australia	–	SDSMGS	0.12	0.08	–	0.21	–	0.16	23
BRHX	Australia	–	AMM	0.34	0.16	–	–	–	0.42	24
ZX	Australia	1267	AMM1	0.20	0.32	0.00	–	0.00	0.36	25
ZX	Australia	2842	AM	0.34	–	–	–	–	0.34	5
ZX	Australia	2842	AMP	0.27	–	–	0.23	–	0.27	5
ZX	Australia	2842	AMM	0.23	0.24	–	–	–	0.35	5
ZX	Australia	2842	AMM1	0.59	0.49	–0.74	–	–0.40	0.24	5
ZX	Australia	2842	AMMP1	0.25	0.11	–	0.14	–	0.31	5
ZX	Australia	2842	AMMP	0.58	0.36	–0.78	0.11	–0.36	0.23	5
ZX	Australia	2842	*AMMP1	0.21	0.11	–	0.17	–	0.27	9
ZX	Australia	2842	*AMMP	0.41	0.28	–0.70	0.15	–0.24	0.19	9
WOKA	Australia	3191	*AMMP1	0.31	0.06	–	0.10	–	0.34	8

Breeds: HEF, Hereford; PHEF, Polled Hereford; CHEF, Canadian Hereford; ANG, Angus; RANG, Red Angus; SIM, Simmental; SGT, Santa Gertrudis; LIM, Limousin; BRG, Brangus; BM, Beefmaster; SNP, Senepol; BRH, Brahman; NLR, Nelore; Xbred, crossbred; AX, Africander cross; HSX, Hereford Shorthorn cross; BRHX, Brahman cross; ZX, zebu cross; WOKA, Wokalup, a synthetic breed formed by mating Charlais X Brahman bulls with Friesian X Angus or Hereford cows.

Models: AMMP, animal model with permanent environmental dam effect and maternal genetic effect & $\sigma_{AM} \neq 0$; SDSMGS, sire-dam model and sire maternal grandsire model; AM, simple animal model; AMP, animal model with a permanent environmental dam effect; AMM, animal model with maternal genetic effect and $\sigma_{AM}=0$; AMM1, animal model with maternal genetic effects & $\sigma_{AM} \neq 0$; AMMP1, animal model with permanent environmental dam effect and maternal genetic effect & $\sigma_{AM}=0$; SMGS, sire-maternal grandsire model; MTPEA, multiple trait pseudo-expectation approach.

References: 1, Skaar (1985); 2, Cantet et al. (1988); 3, Koch (1989) cited by Meyer (1992); 4, Brown et al. (1990); 5, Meyer (1992); 6, Johnson et al. (1992); 7, Johnston et al. (1992b); 8, Meyer et al. (1992a); 9, Meyer et al. (1992b); 10, Winder et al. (1990); 11, Quaas et al. (1985); 12, Graser and Hammond (1985); 13, Wright et al. (1987); 14, Garrick et al. (1989); 15, Perez-Camara (1990); 16, Mrode and Thompson (1990); 17, Swalve (1992); 18, Kriese et al. (1991); 19, Bertrand and Benyshek (1987); 20, Wright et al. (1991); 21, Robinson and Rourke (1992); 22, Eler et al. (1992); 23, Hetzel et al. (1990); 24, Robinson (1990); 25, Mackinnon et al. (1991).

* Bivariate.

See Table 6 for symbols used.

Table 8. Genetic parameter estimates due to maternal effects on yearling weight

Breed	Country	No.	Model	Estimate						Reference
				h^2_A	h^2_M	r_{AM}	c^2	c_{AM}	h^2_T	
HEF	Australia	1449	AM	0.21	–	–	–	–	0.21	1
HEF	Australia	1449	AMP	0.14	–	–	0.09	–	0.14	1
HEF	Australia	1449	AMM	0.12	0.10	–	–	–	0.17	1
HEF	Australia	1449	AMM1	0.15	0.14	–0.41	–	–0.06	0.14	1
HEF	Australia	1449	AMMP	0.12	0.07	–	0.04	–	0.15	1
HEF	Australia	1449	AMMP1	0.16	0.11	–0.48	0.05	–0.06	0.12	1
HEF	Australia	419	AM	0.27	–	–	–	–	0.27	2
PHEF	Australia	1229	*AMMP	0.19	0.15	–	0.08	–	0.27	3
ANG	Australia	2374	AM	0.50	–	–	–	–	0.50	1
ANG	Australia	2374	AMP	0.44	–	–	0.06	–	0.44	1
ANG	Australia	2374	AMM	0.40	0.08	–	–	–	0.44	1
ANG	Australia	2374	AMM1	0.32	0.06	0.45	–	0.06	0.44	1
ANG	Australia	2374	AMMP	0.40	0.05	–	0.03	–	0.43	1
ANG	Australia	2374	AMMP1	0.33	0.04	0.49	0.03	0.05	0.43	1
ANG	Australia	2374	*AMMP	0.41	0.02	–	0.02	–	0.42	4
SIM	UK	4461	AM	0.30	–	–	–	–	0.30	5
SIM	UK	5890	AM	0.31	–	–	–	–	0.31	6
SIM	UK	5890	AMP	0.26	–	–	0.05	–	0.26	6
SIM	UK	5890	AMM	0.27	0.03	–	–	–	0.29	6
SIM	Australia	52 097	AMMP1	0.37	0.11	–0.22	0.01	–0.05	0.36	7
ZX	Australia	1267	AMM1	0.25	0.20	0.01	–	0.01	0.36	8
ZX	Australia	2480	AM	0.27	–	–	–	–	0.27	1
ZX	Australia	2480	AMP	0.22	–	–	0.10	–	0.22	1
ZX	Australia	2480	AMM	0.18	0.12	–	–	–	0.23	1
ZX	Australia	2480	AMM1	0.24	0.17	–0.38	–	–0.08	0.21	1
ZX	Australia	2480	AMMP	0.18	0.10	–	0.03	–	0.23	1
ZX	Australia	2480	AMMP1	0.25	0.14	–0.39	0.03	–0.07	0.21	1
ZX	Australia	2480	*AMMP	0.20	0.07	–	0.06	–	0.24	4
ZX	Australia	2480	*AMMP1	0.24	0.09	–0.35	0.08	–0.05	0.21	4
BRH	Australia	1052	AM	0.36	–	–	–	–	0.36	9
BRH	Australia	1052	AMM	0.30	0.06	–	–	–	0.33	9
NLR	Brasil	7415	–	0.18	0.18	–0.91	–	–	0.02	10
BRHX	Australia	–	AMM	0.21	0.12	–	–	–	0.27	11
Xbred	Australia	1170	AM	0.41	–	–	–	–	0.41	9
Xbred	Australia	1170	AMM	0.20	0.14	–	–	–	0.27	9
WOKA	Australia	1373	*AMM	0.34	0.13	–	–	–	0.41	3

Breeds: HEF, Hereford; PHEF, Polled Hereford; ANG, Angus; SIM, Simmental; ZX, zebu cross; BRH, Brahman; NLR, Nelore; BRHX, Brahman cross; Xbred, crossbred consisting of 1/2 or 3/4 Brahman and 1/2, 3/4, 7/8 or 15/16 Sahiwal crosses with Beef Shorthorn; WOKA, Wokalup, a synthetic breed formed by mating Charolais X Brahman bulls with Friesian X Angus or Hereford cows.

Models: AM, animal model (simple); AMP, animal model with permanent environmental dam effect; AMM, animal model with maternal genetic effect and =0; AMM1, animal model with maternal genetic effect and $\sigma_{AM} \neq 0$; AMMP, animal model with permanent environmental damσ_{AM} effect and maternal genetic effect and $\sigma_{AM}=0$; AMMP1, animal model with permanent environmental dam effect and maternal genetic effect and $\sigma_{AM} \neq 0$.

References: 1, Meyer (1992); 2, Meyer et al. (1991); 3, Meyer et al. (1992a); 4, Meyer et al. (1992b); 5, Perez Camara (1990); 6, Mrode and Thompson (1990); 7, Swalve (1992); 8, Mackinnon et al. (1991); 9, Robinson and Rourke (1992); 10, Eler et al. (1992); 11, Robinson (1990).

See Table 6 for symbols used.

* Bivariate.

Table 9. Average genetic parameter estimates due to maternal effects on growth traits

Parameter		Birth weight	Weaning weight	Yearling weight
h^2_A	No.[a]	43	53	35
	Average	0.30	0.22	0.31
	Range	0.14-0.61	0.07-0.66	0.12-0.50
h^2_M	No.	38	41	23
	Average	0.10	0.13	0.11
	Range	0.03-0.82	0.04-0.49	0.02-0.20
r_{AM}	No.	27	26	10
	Average	–0.35	–0.15	–0.26
	Range	–1.05-0.55	–0.91-0.26	–0.91- 0.49
c^2	No.	18	24	15
	Average	0.03	0.07	0.03
	Range	–0.38-0.18	–0.39-0.29	0.01-0.10
c_{AM}	No.	16	20	9
	Average	–0.06	–0.07	–0.04
	Range	–0.24-0.05	–0.40-0.04	–0.08-0.06
h^2_T	No.	43	53	35
	Average	0.27	0.23	0.31
	Range	–0.02-0.68	0.02-0.81	0.02-0.50

[a] No. of studies.

Symbols used: h^2_A, direct heritability; h^2_M, maternal heritability; r_{AM}, direct-maternal genetic correlation; c^2, maternal environmental variance as a proportion of the penotypic variance; c_{AM}, direct-maternal genetic covariance as a proportion of the phenotypic variance; h^2_T, heritability for the total additive effects.

Table 10. Repeatability estimates for birth, weaning and yearling weights (as traits of the dam)

Breed	Country	Method	Estimate			Reference
			Males	Females	Combined	
Birth Weight						
HEF	USA	a	–	–	0.11-0.24 (281)	1
HEF	USA	a	–	–	–0.03 (74)	1
HEF	USA	–	–	–	0.21 (4423)	2
ANG	USA	b	0.26±0.04	0.29±0.04	–	3
BSHH	Canada	b	–	–	0.41±0.04 (892)	4
GHEF	USA	c	0.14 (620)	–	–	5
GHEF	USA	b	0.18 (620)	–	–	5
HEF, ANG & RANG	USA	b	–	–	0.22±0.02 (5068)	6
Weaning weight						
HEF	USA	a	0.49 (911)	–	–	7
HEF	USA	a	–	–	0.37-0.50 (270)	1
HEF	USA	a	–	–	0.43 (69)	1
HEF	USA	b	–	–	0.52 (745)	8
HEF	USA	b	0.42±0.04 (1915)	–	–	9
HEF	UK	b	–	–	0.42±0.04 (693)	10
HEF	USA	b	0.27±0.003 *(9999)	–	–	11
HEF	USA	b	–	0.50±0.04 (634)	–	12
HEF	USA	–	–	–	0.30 (4423)	2
ANG	USA	b	0.52±0.13 (436)	–	–	9
AANG	UK	b	–	–	0.39±0.05 (607)	10
ANG	USA	b	–	0.26±0.02 (4722)	–	13
ANG	USA	b	–	0.25±0.02 (4722)	–	13
ANG	USA	b	0.19±0.002 *(9906)	–	–	11
ANG	USA	b	–	0.27±0.02 (2644)	–	12
ANG	USA	b	0.43±0.05	0.28±0.04	–	3
SIM	USA	d	–	–	0.21 (114 899)	14
BSHH	Canada	b	–	–	0.25±0.05 (892)	4
LNR	UK	b	–	–	0.49±0.04 (896)	10
GHEF	USA	b	0.43 (603)	–	–	5
GHEF	USA	c	0.49 (603)	–	–	5
GHEF	USA	b	0.51 *(317)	–	–	15
GHEF	USA	b	0.34 *(256)	–	–	15
HEF & ANG	USA	b	0.42±0.04 (2351)	–	–	9
HEF, LNR & AANG	UK	b	0.43±0.02 (2196)	–	–	10
HEF & ANG	USA	c	–	–	0.48 (4838)	16
Yearling weight						
ANG	USA	b	0.21±0.04	0.48±0.04	–	3

Breeds: HEF, Hereford; ANG, Angus; BSHH, Beef Shorthorn; GHEF, Grade Hereford; RANG, Red Angus; AANG, Aberdeen-Angus; SIM, Simmental; LNR, Lincoln Red.

Method: a, correlation between consecutive records of the same cow; b, intraclass correlation; c, regression of later/subsequent records on earlier records of the same cow; d, restricted maximum likelihood.

References: 1, Gregory et al. (1950); 2, Cantet et al. (1988); 3, Alenda and Martin (1987); 4, Fahmy and Lalande (1973); 5, Botkin and Whatley (1953); 6, Bourdon and Brinks (1982); 7, Koger and Knox (1947); 8, Koch (1951); 9, Minyard and Dinkel (1965); 10, Kilkenny (1968); 11, Sellers et al. (1970); 12, Boston et al. (1975); 13, Hohenboken and Brinks (1969); 14, Wright et al. (1987); 15, Rollins and Wagnon (1956); 16, Cunningham and Henderson (1965b).

Figures in parentheses indicate number of observations.

*Steers

Table 11. Phenotypic, genetic and environmental correlations between birth weight and weaning weight

Breed	Country	Estimate									Reference
		Males			Females			Combined			
		r_P	r_A	r_E	r_P	r_A	r_E	r_P	r_A	r_E	
HEF	USA	–	0.99±0.01 (414)	–	–	–	–	–	–	–	1
HEF	USA	–	–	–	0.31 (748)	0.69	0.19	–	–	–	2
HEF	USA	0.35 (1769)	0.41	–	0.43 (1693)	0.53	–	–	–	–	3
HEF	UK	–	–	–	–	–	–	0.23	0.18±0.08	–	4
HEF	USA	–	–	–	–	0.48 (377)	–	–	–	–	5
HEF	USA	0.30	0.37±0.17 (1379)	–	–	–	–	–	–	–	6
HEF	USA	–	0.56±0.12	0.23	–	0.57±0.13	0.28	–	–	–	7
ANG	USA	0.33 (1101)	0.44±0.20	–	0.46 (1012)	0.61±0.26	–	0.39 (2113)	0.53±0.14	–	6
ANG	USA	0.35 (717)	0.59	–	–	–	–	–	–	–	8
ANG	USA	0.34	0.57±0.10	–	0.40	0.36±0.10	–	–	–	–	9
RANG	USA	–	–	–	–	–	–	0.38 (41 184)	0.56±0.02	0.25	10
SIM	USA	–	–	–	–	–	–	0.34 (5578)	0.33±0.11	–	11
SIM	USA	–	0.42±0.12	–	–	0.30±0.10	–	–	0.33±0.07 (17 297)	–	12
CHA	UK	–	–	–	–	–	–	0.23	–0.36±0.22	–	4
CHA	France	0.11 (647)	0.25±0.34	–	–	–	–	–	–	–	13
CHA	Canada	–	–	–	–	–	–	0.34 (1419)	0.47	0.32	14
SGT	USA	0.31 (939)	0.43±0.21	–	0.27 (955)	0.33±0.22	–	0.29 (1894)	0.40±0.14	–	15
IH	Canada	–	–	–	–	–	–	0.29 (892)	0.77±0.11	–	16
/	Nigeria	–	–	–	–	–	–	0.94 (31 488)	0.83±0.02	–	17
u	Nigeria	–	–	–	–	–	–	0.92 (23 708)	0.81±0.01	–	17
; G & NG	USA	0.38	0.63±0.08	0.08	0.41	0.60±0.09	0.20	–	–	–	18
; G & NG	USA	–	–	–	0.31 (779)	0.25±0.26	0.33	–	–	–	19
A, & I	France	0.18 (2673)	0.46±0.16	–	–	–	–	–	–	–	13
	Australia	–	–	–	–	–	–	0.43 (1267)	0.57	–	20
)	Canada	–	–	–	0.46 (505)	0.43±0.28	–	–	–	–	21

ds: HEF, Hereford; ANG, Angus; RANG, Red Angus; SIM, Simmental; CHA, Charolais; SGT, Santa Gertrudis; BSHH, Beef Shorthorn; SDV, South Devon; LIM, Limousin; BA, Blonde d'Aquitaine; ZX, zebu cross; SBP, synthetic beef cattle population with approximately 33% Charolais, 33% Angus and 20% Galloway breeding with small contributions from other beef breeds.

mates: r_P, phenotypic correlation; gr_A, enetic correlation; r_E, environmental correlation.

erences: 1, Lasley et al. (1961); 2, Swiger (1961); 3, Koch et al. (1973); 4, Pabst et al. (1977); 5, Koch (1978); 6, Nelsen and Kress (1979); 7, Buchanan et al. (1982); 8, Knights et al. (1984); 9, Alenda and Martin (1987); 10, Winder et al. (1990); 11, Burfening et al. (1978a); 12, Burfening et al. (1978b); 13, Renand (1985); 14, Johnston et al. (1992); 15, Aaron et al. (1987); 16, Fahmy and Lalande (1973); 17, Iloeje (1986); 18, Bourdon and Brinks (1982); 19, Smith et al. (1989); 20, Mackinnon et al. (1991); 21, Arthur and Makarechian (1992).

ires in parentheses indicate number of observations.

Table 12. Phenotypic, genetic and environmental correlations between birth weight and yearling weight

Breed	Country	Estimate									Reference
			Males			Females			Combined		
		r_P	r_A	r_E	r_P	r_A	r_E	r_P	r_A	r_E	
HEF	UK	–	–	–	–	–	–	0.25	0.26±0.09	–	1
HEF	USA	–	–	–	–	0.60 (377)	–	–	–	–	2
HEF	USA	–	0.63±0.13	0.28	–	0.58±0.12	0.34	–	–	–	3
ANG	USA	0.43 (717)	0.57	–	–	–	–	–	–	–	4
ANG	USA	0.37	0.75±0.11	–	0.35	0.45±0.09	–	–	–	–	5
RANG	USA	–	–	–	–	–	–	0.39 (41 184)	0.57±0.02	0.25	6
CHA	France	0.18 (699)	0.27	–	–	–	–	–	–	–	7
CHA	Canada	–	–	–	–	–	–	0.37 (1418)	0.46	0.35	8
HEF, ANG & RANG	USA	0.41	0.69±0.08	–0.01	0.40	0.55±0.11	0.25	–	–	–	9
HEF, ANG & RANG	USA	–	–	–	0.35 (779)	0.41±0.19	0.33	–	–	–	10
ZX	Australia	–	–	–	–	–	–	0.35 (1267)	0.47	–	11
SBP	Canada	–	–	–	0.45 (505)	0.53±0.19	–	–	–	–	12

Breeds: HEF, Hereford; ANG, Angus; RANG, Red Angus; CHA, Charolais; ZX, Zebu cross; SBP, synthetic beef cattle population with approximately 33% Charolais, 33% Angus and 20% Galloway breeding with small contributions from other beef breeds.
Estimates: , r_P phenotypic correlation; r_A, genetic correlation; r_E, environmental correlation.
References: 1, Pabst et al. (1977); 2, Koch (1978); 3, Buchanan et al. (1982); 4, Knights et al. (1984); 5, Alenda and Martin (1987); 6, Winder et al. (1990); 7, Renand and Gillard (1982); 8, Johnston et al. (1992); 9, Bourdon and Brinks (1982); 10, Smith et al. (1989); 11, Mackinnon et al. (1991); 12, Arthur and Makarechian (1992).
Figures in parentheses indicate number of observations.

Table 13. Phenotypic, genetic and environmental correlations between weaning weight and yearling weight

Breed	Country	Estimate									Reference
			Males			Females			Combined		
		r_P	r_A	r_E	r_P	r_A	r_E	r_P	r_A	r_E	
HEF	USA	0.70 *(499)	0.10	0.76	0.57 (420)	0.18	1.07	0.65 (919)	0.16	0.83	1
HEF	UK	–	–	–	–	–	–	0.61	0.58±0.06	–	2
HEF	USA	–	–	–	–	0.71 (377)	–	–	–	–	3
HEF	USA	–	0.61±0.11	0.71	–	0.74±0.11	0.73	–	–	–	4
ANG	USA	0.71 (717)	0.79	–	–	–	–	–	–	–	5
ANG	USA	0.77	0.89±0.05	–	0.71	0.76±0.07	–	–	–	–	6
AANG	UK	–	–	–	–	–	–	0.57	0.38±0.12	–	2
RANG	USA	–	–	–	–	–	–	0.63 (41 184)	0.78±0.02	0.57	7
SIM	Canada	–	–	–	–	–	–	–	0.63 (27 788)	–	8
SIM	UK	–	–	–	–	–	–	0.63 (4461)	0.92	0.48	9
CHA	Canada	–	–	–	–	–	–	0.69 (1418)	0.47	0.73	10
DEV	UK	–	–	–	–	–	–	0.66	0.68±0.09	–	2
SDV	Nigeria	–	–	–	–	–	–	0.83 (23 708)	0.74±0.02	–	11
SSX	UK	–	–	–	–	–	–	0.57	0.37±0.15	–	2
Zebu	Nigeria	–	–	–	–	–	–	0.85 (31 488)	0.74±0.02	–	11
HEF & AANG	Canada	–	–	–	–	–	–	0.73 (84 021)	0.80	0.71	12
HEF, ANG & RANG	USA	0.76	0.89±0.03	0.51	0.76	0.90±0.03	0.46	–	–	–	13
HEF, ANG & RANG	USA	–	–	–	0.79 (779)	0.84±0.09	0.79	–	–	–	14
ZX	Australia	–	–	–	–	–	–	0.76 (1267)	0.84	–	15
SBP	Canada	–	–	–	0.66 (505)	0.36±0.31	–	–	–	–	16

Breeds: HEF, Hereford; ANG, Angus; AANG, Aberdeen-Angus; RANG, Red Angus; SIM, Simmental; CHA, Charolais; DEV, Devon; SDV, South Devon; SSX, Sussex; ZX, zebu cross; SBP, synthetic beef cattle population with approximately 33% Charolais, 33% Angus and 20% Galloway breeding with small contributions from other beef breeds.

Estimates: r_P, phenotypic correlation; r_A, genetic correlation; r_E, environmental correlation.

References: 1, Blackwell et al. (1962); 2, Pabst et al. (1977); 3, Koch (1978); 4, Buchanan et al. (1982); 5, Knights et al. (1984); 6, Alenda and Martin (1987); 7, Winder et al. (1990); 8, Schaeffer and Wilton (1981); 9, Perez-Camara (1990); 10, Johnston et al. (1992); 11, Iloeje (1986); 12, Kennedy and Henderson (1975b); 13, Bourdon and Brinks (1982); 14, Smith et al. (1989); 15, Mackinnon et al. (1991); 16, Arthur and Makarechian (1992).

Figures in parentheses indicate number of observations.

* Steers.

Table 14. Average phenotypic, genetic and environmental correlations between various growth traits

Traits correlated		Males		Females		Steers		Combined	
		Average	Range	Average	Range	Average	Range	Average	Range
Birth weight	*r_P	0.30(9)	0.11-0.38	0.39(8)	0.27-0.46	–	–	0.65(9)	0.23-0.94
and	r_A	0.47(11)	0.25-0.99	0.41(10)	0.25-0.69	–	–	0.63(10)	-0.36-0.83
weaning weight	r_E	0.16(2)	0.08-0.23	0.22(3)	0.19-0.33	–	–	0.25(2)	0.25-0.34
Birth weight	r_P	0.37(4)	0.18-0.43	0.39(4)	0.35-0.45	–	–	0.39(3)	0.25-0.39
and	r_A	0.64(4)	0.27-0.75	0.51(5)	0.41-0.60	–	–	0.56(3)	0.26-0.57
yearling weight	r_E	0.14(2)	0.01-0.28	0.27(2)	0.25-0.34	–	–	0.25(2)	0.25-0.35
Weaning weight	r_P	0.76(3)	0.70-0.77	0.73(5)	0.57-0.79	0.70(1)	–	0.74(8)	0.57-0.85
and	r_A	0.88(3)	0.61-0.89	0.76(6)	0.18-0.90	0.10(1)	–	0.76(9)	0.16-0.92
yearling weight	r_E	0.61(2)	0.51-0.71	0.59(3)	0.46-1.07	0.76(1)	–	0.66(5)	0.48-0.83

Figures in parentheses indicate number of studies.
*r_P, phenotypic correlation; r_A, genetic correlation; r_E, environmental correlation.

Table 15. Phenotypic, genetic and environmental correlations between birth, weaning and yearling weights and ultrasonic fat depth and muscling score

Breed	Country	Estimate									Reference
		Males			Females			Combined			
		r_P	r_A	r_E	r_P	r_A	r_E	r_P	r_A	r_E	
Birth weight and muscling score											
HEF	USA	–	–	–	–	0.16 (377)	–	–	–	–	1
HEF	USA	–	0.18±0.16	0.10	–	0.12±0.19	0.05	–	–	–	2
CHA	France	0.08 (699)	0.38±0.28	–	–	–	–	–	–	–	3
BA, CHA & LIM	France	0.00 (3098)	–0.03±0.16	–	–	–	–	–	–	–	3
Weaning weight and fat depth											
HEF	USA	0.26 (578)	–0.01±0.63	–	–	–	–	–	–	–	4
HEF	USA	0.19 (824)	0.13±0.53	–	–	–	–	–	–	–	5
GHEF	USA	-0.13 *(679)	–1.00	–	–	–	–	–	–	–	6
Weaning weight and muscling score											
HEF	USA	-0.02 *(499)	–0.48	0.09	–0.15 (420)	–0.68	0.10	–0.07 (919)	–0.56	0.10	7
HEF	USA	–	–	–	–	–0.07 (377)	–	–	–	–	1
HEF	USA	–	–0.24±0.20	0.35	–	0.21±0.22	0.36	–	–	–	2
HEF	USA	0.21 *(341)	0.38	–	–	–	–	–	–	–	6
HA	France	0.03 (699)	–0.04±0.36	–	–	–	–	–	–	–	3
A, HA & IM	France	–0.01 (3098)	–0.10±0.15	–	–	–	–	–	–	–	3
earling weight and fat depth											
EF	USA	0.28 (695)	0.29±0.51	–	–	–	–	–	–	–	8
EF	USA	0.29 (578)	0.19±0.43	–	–	–	–	–	–	–	4
EF, NG & HEF	Australia	–	–	–	–	–	–	–	0.10 (9232)	0.34	9
earling weight and muscling score											
EF	USA	0.27 *(499)	–0.66	0.27	–0.12 (420)	–0.77	0.58	–0.01 (919)	–0.65	0.35	7
EF	USA	–	–	–	–	–0.19 (377)	–	–	–	–	1
EF	USA	–	–0.14±0.20	0.56	–	0.04±0.03	0.56	–	–	–	2
HA	France	0.27 (699)	0.08	–	–	–	–	–	–	–	10
EF, NG & HEF	Australia	–	–	–	–	–	–	–	0.11 (3870)	0.29	9

Fat depth and muscling score

GHEF	USA	–0.09 *(341)	–0.46	–	–	–	–	–	–	–	6
HEF, ANG & PHEF	Australia	–	–	–	–	–	–	–	0.08 (3870)	0.10	9

Breeds: HEF, Hereford; CHA, Charolais; BA, Blonde d'aquitaine; LIM, Limousin; GHEF, Grade Hereford; PHEF, Polled Hereford; ANG, Angus.

Estimates: r_P, phenotypic correlation; r_A, genetic correlation; r_E, environmental correlation.

References: 1, Koch (1978); 2, Buchanan et al. (1982); 3, Renand (1985); 4, Neely et al. (1982); 5, Lamb et al. (1990); 6, Dinkel and Busch (1973); 7, Blackwell et al. (1962); 8, Mavrogenis et al. (1978); 9, Robinson et al. (1992); 10, Renand and Gaillard (1982).

Figures in parentheses indicate number of observations.

*Steers.